Detritivores of the South American Fish Family Prochilodontidae (Teleostei: Ostariophysi: Characiformes): A Phylogenetic and Revisionary Study

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and
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ABSTRACT

Castro, Ricardo M.C., and Richard P. Vari. Detritivores of the South American Fish Family Prochilodontidae (Teleostei: Ostariophysi: Characiformes): A Phylogenetic and Revisionary Study. *Smithsonian Contributions to Zoology,* number 622, 189 pages, 71 figures, 23 tables. 2004.—The investigation of the inter- and intrafamilial relationships of the Prochilodontidae was investigated based on information from osteological and soft anatomical systems. Synapomorphies uncovered during this study provide additional evidence that (1) the clade formed by the Prochilodontidae plus Curimatidae is the sister group to the clade that consists of the Anostomidae plus Chilodontidae, (2) supports the hypothesis of the monophyly of the Prochilodontidae, *Ichthyoelephas* Posada Arango (1909), *Prochilodus* Agassiz (in Spix and Agassiz, 1829), and *Semaprochilodus* Fowler (1941), (3) demonstrates that *Prochilodus* is the sister group to the clade formed by *Ichthyoelephas* plus *Semaprochilodus,* and (4) partially resolves interspecific relationships.

Recognized genera of the Prochilodontidae are *Ichthyoelephas, Prochilodus,* and *Semaprochilodus. Pacu* Agassiz (in Spix and Agassiz, 1829) and *Chilomyzon* Fowler (1906) are synonyms of *Prochilodus.*

Ichthyoelephas includes two species: *I. humeralis* (Günther, 1859); and *I. longirostris* (Steindachner, 1879). *Ichthyoelephas pataló* Posada Arango (1909) and *I. longirostris neglectus* Dahl (1971) are synonyms of *I. longirostris.*

Prochilodus consists of thirteen species: *P. argenteus* Agassiz (in Spix and Agassiz, 1829); *P. brevis* Steindachner (1874); *P. britskii* Castro (1993); *P. costatus* Valenciennes (in Cuvier and Valenciennes, 1850); *P. hartii* Steindachner (1874); *P. lacustris* Steindachner (1907); *P. lineatus* (Valenciennes, 1836); *P. magdalenae* Steindachner (1879); *P. mariae* Eigenmann (1922); *P. nigricans* Agassiz (in Spix and Agassiz, 1829); *P. reticulatus* Valenciennes (1850); *P. rubrotaeniatus* Jardine (1841); and *P. vimboides* Kner (1859).

Semaprochilodus contains six species: *S. brama* (Valenciennes, in Cuvier and Valenciennes, 1850); *S. insignis* (Jardine, 1841); *S. kneri* (Pellegrin, 1909); *S. laticeps* (Steindachner, 1879); *S. taeniurus* (Valenciennes, in Humboldt and Bonpland, 1817); and *S. varii* Castro (1988). *Semaprochilodus squamilentus* Fowler (1941) is a synonym of *S. brama. Prochilodus theraponura* Fowler (1906) and *P. amazonensis* Fowler (1906) are synonyms of *Semaprochilodus insignis.*

Keys are provided to the genera and species of prochilodontids. Neotypes are designated for *Prochilodus argenteus* and *P. nigricans.* Lectotypes are designated for *Prochilodus affinis, P. asper, P. brevis, P. cearensis, P. hartii, P. humeralis, P. kneri, P. lacustris, P. longirostris, P. asper* var. *magdalenae, P. oligolepis, P. reticulatus, P. scrofa,* and *P. vimboides.*

The phylogenetic biogeography of the Prochilodontidae indicates that the family dates back minimally to approximately 12 million years ago, with higher level intrafamilial cladogenic events also dating to at least that time period; these dates are congruent with data from the fossil record for more encompassing groups within the Characiformes. Major shifts of overall bauplan characterize the Prochilodontidae and the major clades within the family, but there is relatively little interspecific diversity. The *Prochilodus* bauplan has apparently been static for at least 12 million years.

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Detritivores of the South American Fish Family Prochilodontidae (Teleostei: Ostariophysi: Characiformes): A Phylogenetic and Revisionary Study

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Introduction

Fishes of the family Prochilodontidae are the most important component of the commercial and subsistence fisheries in South American freshwaters, an ecosystem in which they inhabit both lotic and lentic habitats and achieve moderate to large body sizes (74 cm TL in *Prochilodus lineatus* (Sverlij et al., 1993:36) and more than 80 cm TL in *Ichthyoelephas longirostris* (Patiño R., 1973:82)). West of the Andean Cordilleras prochilodontids have a disjunct distribution in the Lago Maracaibo drainage system of Venezuela and Colombia, the Caribbean versant rivers of northwestern Colombia, and the Pacific slope drainages of western Ecuador. Prochilodontids are unknown from the Trans-Andean portions of Peru and all of Chile, the only country on the continent from which the family is absent. East of the Andean Cordilleras the Prochilodontidae inhabit much of South America with three notable exceptions: the cooler, often more xeric southern portions of the continent, the relatively small Caribbean versant rivers of the northern portion of the continent east of Lago Maracaibo, and the series of Brazilian Atlantic coastal rivers between the Rio Paraíba do Sul and the Laguna dos Patos basin. Most of the remaining lacunae in the known distribution of prochilodontids east of the Andean Cordilleras (e.g., portions of the Rio Madeira basin) probably reflect the limited ichthyological collecting efforts in those regions rather than the actual absence of members of the family. Such sampling problems are pervasive for many components of the speciose Neotropical freshwater fish fauna (Vari and Malabarba, 1998:9).

Prochilodontids, with their highly restructured lips, teeth, and jaws, are readily distinguishable externally from the remainder of the Neotropical ichthyofauna and, indeed, from all other fishes. Except as larvae, prochilodontids have unusual fleshy lips equipped with two series of numerous, relatively small, falciform or spatulate teeth movably attached to the lips rather than to the jaw bones. Upon jaw protraction these distinctive lips form an oral disk bordered by a ring of small teeth. The dramatically restructured lips, teeth, and jaws of prochilodontids are paralleled by pronounced modifications of multiple components of the gill arches and suspensorium, the most obvious of which are the well-developed, dorsally situated, sac-like, epibranchial organs (Menin and Mimura, 1991, fig. 1). Similarly, the prochilodontid digestive tract demonstrates specializations of the stomach, pyloric caeca, and intestines, most strikingly the elaboration and elongation of the two latter systems (Angelescu and Gneri, 1949:214–238; Bowen, 1984:139–142; Menin and Mimura, 1991, fig. 15).

The suite of modifications of the jaws, gill arches, and digestive system characteristic of prochilodontids allows them to efficiently gather and process their two primary food items, detritus and aufwucks (Araújo-Lima et al., 1986; Bowen, 1984; Bowen et al., 1984). Detritus, which is altered dead organic matter, and aufwucks (periphyton), which are the plants, animals, and detritus that adhere to vegetation, rocks, and other exposed surfaces in the aquatic environment, are major nutritional resources in the Neotropics, both in permanent fresh wa-

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ters (Flecker, 1996:1845) and in the seasonally flooded rain forest (Goulding et al., 1988:61–62, fig. 6.1).

Notwithstanding the prevalence of detritus and aufwucks in myriad aquatic systems, most fishes lack the prerequisite anatomical and physiological adaptations to exploit those resources. Rather, invertebrates are typically the dominant detritivores in most fresh-water systems and are, in turn, exploited by fishes and other predators. Prochilodontids and curimatids, as detritivores, skip the intermediate step in the food chain of insect detritivory and directly utilize detritus and aufwucks. Access to the abundant energy sources present in detritus and aufwucks undoubtedly accounts for the prominence of the Prochilodontidae and Curimatidae among Neotropical freshwater fishes. Both families are the major, and in some settings the dominant, components of the Neotropical freshwater ichthyofauna (Bowen, 1984). *Prochilodus lineatus,* the prime example, was estimated by Bonetto (1975, 1994; cited therein as *P. platensis*) to constitute more than 60% of the total ichthyomass throughout the vast expanse of the lower Rio Parana basin.

As would be expected, the prominence of the Prochilodontidae in the ichthyofauna of many lowland aquatic systems in the Neotropics is paralleled by the importance of members of that family in commercial fisheries. In the lower Rio Negro of Brazil, more than 90% of the commercial catch consists of two *Semaprochilodus* species (Goulding et al., 1988:61, fig. 6.1), with prochilodontids becoming progressively more important in the commercial fisheries of the central portion of the Amazon Basin (Ribeiro and Petrere, 1990:196). In northern South America, *Prochilodus magdalenae* represents 47% of the fishery in the Trans-Andean Río Sinú (Olaya-Nieto et al., 2001: 43), whereas in the Río Apure drainage of Venezuela prochilodontids, which represent only two of the more than 350 species in that basin, "routinely take first place in terms of tons landed" and are equally important in the subsistence fishery (Taphorn, 1992:482). In the southern portion of the distribution of the family, Sverlij et al. (1993:51) reported that *Prochilodus lineatus* "constitutes 40% of the total fishery in the Río Paraná, 86% of the fishery in the Río de La Plata, and 95% of the fishery in the Río Uruguay" (our translation; value for the Rio Uruguay is for the lower portion of that basin). Other prochilodontid species are similarly important in both the commercial and subsistence fisheries of various river systems in Colombia (Dahl, 1971:xvi; Sánchez, M. et al., 2000:218), Venezuela (Espinosa and Gimenez, 1974:1; Novoa R. et al., 1982:277), and other South American countries (Welcomme, 1979:200), and they have been introduced outside of their native range both in the Neotropics and elsewhere (e.g., Papua New Guinea; Wafy, 2001:2).

The extensive exploitation of many prochilodontids in commercial and subsistence fisheries together with changes in many water systems resulting from human activities has resulted in the danger of at least local extinction of some species (Instituto Alexander von Humboldt, 2000:184). The overall importance of the Prochilodontidae in Neotropical fisheries and attempts to compensate for these adverse anthropogenic impacts are clearly reflected in the numerous studies that involve induced spawning, captive rearing, and marketing of various prochilodontid species (e.g., Antoniutti et al., 1995; Bustamente-Varón et al., 1997; and references therein).

Above and beyond their commercial importance, the sediment-processing activities of at least some prochilodontid species, for example *Prochilodus mariae* in the Río Orinoco basin (Flecker, 1996:1850), makes members of the family significant as a consequence of their functional dominance in some aquatic ecosystems. Experimental studies have demonstrated that prochilodontids are key to the overall structure of the biotic communities in such habitats. The experimental removal of these prochilodontids results both in increased sediment accumulation and in alterations in the composition of the resident invertebrate fauna. As such, *P. mariae* and presumably other prochilodontids serve as ecosystem engineers (sensu Coleman and Williams, 2002), thereby functioning as "keystone" species in those communities. In many settings prochilodontids also are important in the transport of energy both longitudinally and laterally within river systems from nutrient rich to nutrient poor areas where it is stabilized by predators with less pronounced migrations (Winemiller and Jepsen, 1998; Lucas and Baras, 2001).

The huge prochilodontid populations in many South American river systems are famous for the mass migrations associated with feeding and reproduction. In the course of upriver migrations, prochilodontids both overcome obstacles via dramatic leaps of up to several meters (Goulding, 1981:103; see also Godoy, 1975, fig. 151; Mochek and Pavlov, 1998, fig. 2) and travel notable distances (Lucas and Baras, 2001:113). Individuals of *Prochilodus lineatus* in the Rio Paraná undergo daily migrations of up to 43 km (Godoy, 1975:43), and some individuals travel minimally almost 1500 km between their mark and recapture (Sverlij et al., 1993:28). Molecular studies have revealed high levels of intraspecific genetic homogeneity in some prochilodontid species across major river basins (e.g., Río de La Plata system; Revaldaves et al., 1997; Sivasundar et al., 2001). Such high levels of genetic homogeneity indicate that these species have pronounced rates of intra-populational gene flow, an apparent consequence of their wide ranging intra-basin migrations that result in near panmixis across the gene pool.

As emphasized by Mago-Leccia (1972:35), pervasive uncertainty has long characterized the taxonomy of the Prochilodontidae. Indeed, that author proposed that the systematics of the family was among the most confounding in the South American freshwater ichthyofauna. Whether or not this characterization is appropriate, such uncertainty is scientifically unsatisfying. Furthermore, it is problematic for specialists in multiple endeavors in Neotropical aquatic systems (e.g., ecology, resource development and management) in light of the significant role played by prochilodontids in the energy flow within the systems that they inhabit (Jepsen et al., 1997:1085; Winemiller, 1996:303), the economic importance of the family across major portions of South America (see above), and the accelerating adverse impact of anthropogenic activities on many prochilodontid species (Barbarino Duque et al., 1998:33; Mochek and Pavlov, 1998:28).

Synergy of several factors contributed to this unsatisfactory situation. Preeminent was the broad geographic ranges of many prochilodontid species and the consequent difficulty in evaluating the degree of intraspecific ontogenetic and ecophenotypic variation. This intrinsic complication and the typically limited series of specimens available to previous researchers resulted in the description of many nominal forms herein considered to be synonyms of recognized species. A further complication cited by Mago-Leccia (1972:36), and confirmed herein, is the relative homogeneity demonstrated by prochilodontids in many of the features typically useful in discriminating species of other groups of characiforms. Superimposed on the challenges intrinsic to the organisms were the brief, and sometimes uninformative or misleading original descriptions of some nominal prochilodontid species. Those impediments were exacerbated by the location of type series and other historical important specimens in numerous North American and European depositories and/or the loss of type specimens—a situation that rendered it difficult, and sometimes impossible, for previous researchers to examine many critical specimens.

In the only previous in-depth, albeit geographically delimited, revisionary analysis within the Prochilodontidae, Mago-Leccia (1972) critically reviewed the components of the family that occur within Venezuela, resolved the taxonomic questions in six of the 44 nominal prochilodontid species proposed to that date, and highlighted the problematic nature of prochilodontid taxonomy. Castro (1988, 1993) subsequently described two previously unrecognized prochilodontid species. The 36 other nominal species within the family have not been critically analyzed. Our results highlight the pervasive problems within the previous species-level taxonomy of the Prochilodontidae; only 21 of the 46 nominal species within the family, or approximately 46%, are recognized herein as valid (Table 1). Furthermore, most of the species limits recognized herein differ, often to a pronounced extent, from the concepts used by previous authors. As would be expected, given that situation, the distributions for these species also differ significantly from the ranges available from the earlier literature.

The Prochilodontidae has long been de facto delimited as a natural assemblage (monophyletic in the modern sense) in light of its distinctive jaws, lips, and teeth, albeit without the formal identification of familial synapomorphies. Vari (1983:49) defined a series of synapomorphies that diagnose the Prochilodontidae, some of which had been intuitively utilized by previous workers to delimit the group as "natural" within the Characiformes. This stability in the limits of the Prochilodontidae contrasts with the dramatically divergent alternative interpretations of the relationships of the family proposed by different authors. These hypotheses ranged from Boulenger's (1904:576) alignment of the Prochilodontidae with the Old World family Citharinidae to Roberts' (1973:221) proposal of a relationship of the Prochilodontidae with the Neotropical families Anostomidae and Chilodontidae. More recently Géry (1977:210) united the Prochilodontidae, Curimatidae, Chilodontidae, and Anodontinae of Greenwood et el. (1966) into an expanded Curimatidae, but he retained the Anostomidae as a separate family. Except for the hypothesis proposed by Roberts (1973), all of these classifications were advanced without discussions of the evidence that supports the proposed associations of taxa or with, at most, a cursory discussion of the anatomical information that underpins the proposed taxonomic alignments.

A series of synapomorphies identified by Vari (1983:47) indicate that the Prochilodontidae is the sister group of the Curimatidae, a conclusion at variance with Roberts' (1973) alignment of the Prochilodontidae with the Anostomidae and Chilodontidae. Data from molecular analyses (Ortí, 1997; Ortí and Meyer, 1997) provided additional evidence in support of Vari's (1983) morphologically based phylogenetic hypothesis. Vari (1983:46) also discussed evidence for the hypothesis that the clade formed by the Prochilodontidae and Curimatidae is the sister group to a clade formed by the families Anostomidae plus Chilodontidae (Vari, 1983); this hypothesis is supported by an additional synapomorphy identified during this study.

Previous studies neither addressed the phylogenetic relationships within the Prochilodontidae nor the question of the naturalness of the three recognized genera in the family (*Ichthyoelephas, Prochilodus, Semaprochilodus*). Indeed, Géry's (1977:215) suggestion that *Semaprochilodus* is a subunit of *Prochilodus* would likely result in the non-monophyly of *Prochilodus* as now defined. Nonetheless, some external features of *Ichthyoelephas* (the massively developed, fleshy lips) and *Semaprochilodus* (the dark stripes on the anal and caudal fins) appear intuitively to be derived relative to the conditions in proximate characiform outgroups, albeit not previously critically evaluated as to their derived nature. None of the external features of *Prochilodus* represent comparably obvious potential synapomorphies, a situation that raises the question of the potential non-monophyly of that genus.

These interlinked phylogenetic questions are addressed via the examination of a series of skeletal and soft morphological systems to identify phylogenetically informative features in order to (1) test the hypothesis of the monophyly of the Prochilodontidae advanced by Vari (1983); (2) test the monophyly of *Ichthyoelephas, Prochilodus,* and *Semaprochilodus* as now delimited; and (3) develop a hypothesis of intrafamilial phylogenetic relationships.

The resultant hypothesis of intrafamilial phylogenetic relationships serves as the basis for a revisionary study of the Prochilodontidae and for an examination of (1) the validity of species proposed to date, and (2) the phylogenetic biogeography of the family.

Evidence in addition to that discussed by Vari (1983) also was uncovered relative to the hypothesis of the sister-group relationship between the clade formed by the Prochilodontidae and Curimatidae, on the one hand, and the clade that consists of the Anostomidae and Chilodontidae, on the other.

TABLE 1.—Nominal species assigned to the family Prochilodontidae in this and other publications and the recognized equivalent species according to the results of this study. Nominal species are cited as in the original description and are arranged alphabetically by specific epithet.

Nominal species	Assignment herein
Prochilodus affinis Lütken, 1875	*Prochilodus costatus*
Prochilodus amazonensis Fowler, 1906	*Semaprochilodus insignis*
Prochilodus argenteus Agassiz in Spix and Agassiz, 1829	*Prochilodus argenteus*
Prochilodus asper Lütken, 1875	*Prochilodus reticulatus*
Prochilodus asper var. *magdalenae* Steindachner, 1879	*Prochilodus magdalenae*
Prochilodus beani Eigenmann in Eigenmann and Ogle, 1907	*Prochilodus magdalenae*
Prochilodus beni Pearson, 1924	*Prochilodus nigricans*
Prochilodus binotatus Jardine, 1841	nomen dubium[1]
Prochilodus brama Valenciennes, 1850	*Semaprochilodus brama*
Prochilodus brevis Steindachner, 1874	*Prochilodus brevis*
Prochilodus britskii Castro, 1993	*Prochilodus britskii*
Prochilodus caudifasciatus Starks, 1906	*Prochilodus nigricans*
Prochilodus cearensis Steindachner, 1911	*Prochilodus brevis*
Prochilodus cephalotes, Cope, 1878	*Prochilodus nigricans*
Salmo corimbata Kner, 1859	*Prochilodus vimboides*
Prochilodus costatus Valenciennes, 1850	*Prochilodus costatus*
Prochilodus dobulinus Valenciennes, 1850	nomen dubium[2]
Prochilodus eigenmanni Ahl, 1937	*Prochilodus magdalenae*
Prochilodus hartii Steindachner, 1874	*Prochilodus hartii*
Prochilodus humeralis Günther, 1859	*Ichthyoelephas humeralis*
Prochilodus insignis Jardine, 1841	*Semaprochilodus insignis*
Salmo jaraqui Kner, 1859	*Semaprochilodus insignis*
Prochilodus kneri Pellegrin, 1909	*Semaprochilodus kneri*
Prochilodus labeo Loubens et al., 1991	*Prochilodus nigricans*
Prochilodus lacustris Steindachner, 1907	*Prochilodus lacustris*
Prochilodus laticeps Steindachner, 1879	*Semaprochilodus laticeps*
Pacu lineatus Valenciennes, 1836	*Prochilodus lineatus*
Prochilodus longirostris Steindachner, 1879	*Ichthyoelephas longirosris*
Ichthyoelephas longirostris longirostris Dahl, 1971	*Ichthyoelephas longirostris*
Ichthyoelephas longirostris neglectus Dahl, 1971	*Ichthyoelephas longirostris*
Prochilodus margravii	Rejected by ICZN[3]
Prochilodus mariae Eigenmann, 1922	*Prochilodus mariae*
Prochilodus maripicru Eigenmann, 1912	*Prochilodus rubrotaeniatus*
Prochilodus nigricans Agassiz in Spix and Agassiz, 1829	*Prochilodus nigricans*
Salmo novemradiatus Larrañaga, 1923	*Prochilodus lineatus*
Prochilodus oligolepis Günther, 1864	*Prochilodus vimboides*
Prochilodus ortonianus Cope, 1878	*Prochilodus nigricans*
Ichthyoelephas pataló Posada Arango, 1909	*Ichthyoelephas longirostris*
Prochilodus platensis Holmberg, 1888	*Prochilodus lineatus*
Prochilodus pterostigma Fowler, 1913	Non-prochilodontid species[4]
Prochilodus reticulatus Valenciennes, 1850	*Prochilodus reticulatus*
Prochilodus rubrotaeniatus Jardine, 1841	*Prochilodus rubrotaeniatus*
Prochilodus scrofa Steindachner, 1881	*Prochilodus lineatus*
Semaprochilodus squamilentus Fowler, 1941	*Semaprochilodus brama*
Prochilodus steindachneri Fowler, 1906	*Prochilodus vimboides*
Prochilodus steindachneri Eigenmann, 1922	Preoccupied, replaced by *P. eigenmanni*[5]
Prochilodus stigmaturus Fowler, 1911	Non-prochilodontid species[6]
Curimatus taeniurus Valenciennes, 1817	*Semaprochilodus taeniurus*
Prochilodus theraponura Fowler, 1906	*Semaprochilodus insignis*
Curimatus tigris Fowler, 1914	*Prochilodus nigricans*
Semaprochilodus varii Castro, 1988	*Semaprochilodus varii*
Prochilodus vimboides Kner, 1859	*Prochilodus vimboides*

[1] *Prochilodus binotatus* (1841) is apparently a nomen dubium. The description was based upon a mosaic of two or more species. See discussion under *Semaprochilodus insignis*.

[2] *Prochilodus dobulinus* Valenciennes (1850) is apparently a nomen dubium. The description was based upon a mosaic of two or more species. See discussion under *Prochilodus nigricans*.

[3] *Prochilodus margravii* was rejected by ICZN (see under synonymy of *Prochilodus argenteus*).

[4] *Prochilodus pterostigma* Fowler (1913) was transferred by Fowler (1940:68) to the Curimatidae as a possible synonym of *Curimatus bimaculata* Steindachner. Vari (1991:46) confirmed that synonymy and assigned the species to *Steindachnerina* Fowler.

[5] *Prochilodus steindachneri* Eigenmann (1922) was preoccupied by a species of the same name described by Fowler (1906). Ahl (1937) proposed *Prochilodus eigenmanni* as a replacement name to resolve the problem.

[6] *Prochilodus stigmaturus* Fowler (1911) was shown by Vari and Castro (1988) to be a member of the Curimatidae rather than the Prochilodontidae. The species was placed as a junior synonym of *Steindachnerina dobula* (Günther) by Vari (1991:66).

METHODS AND MATERIAL

Characters were typically assigned discrete, usually binary, states to minimize problems with the ambiguous ordering of multistate characters. Data for this analysis was extracted from multiple-body systems in order to minimize the loading that results from functionally constrained correlations and thus to better determine the phylogenetic signal. Whenever possible two or more specimens of each species were cleared and counterstained in order to permit checks for anomalous features. This procedure was impossible for *Prochilodus britskii* and *Ichthyoelephas longirostris* because of the limited available number of suitable specimens of these species.

Hypotheses of relationships were proposed using the cladistic or phylogenetic method first formalized by Hennig (1950, 1966) and subsequently developed by other authors. Parsimony analysis was employed to generate hypotheses of phylogenetic relationships and of character-state transformations using Hennig86, version 1.5 (Farris, 1988). Heuristic search was applied using "mhennig*" and "ie*." Character polarity were determined by outgroup comparison first to the Curimatidae, the sister group to the Prochilodontidae, and second to the clade formed by the Anostomidae and Chilodontidae, which together constitute the sister group to the clade formed by the Curimatidae and Prochilodontidae. All characters were analyzed ordered except where noted otherwise. For the purposes of the analysis, we utilize an artificial, designated outgroup having the primitive conditions cited for each of the characters as discussed above. This avoids the problem of limiting the outgroup to the Curimatidae, which lacks various systems (e.g., oral dentition) that are discretely variable and, thus, phylogenetically informative within the Prochilodontidae. It also obviates the need to include the numerous synapomorphies for the members of the Curimatidae (see Vari, 1983, 1989a) in order to retain that group as monophyletic in light of the occurrence of some derived attributes apparently homoplastically present in subunits of the Curimatidae and Prochilodontidae. In our analysis, in the case of potentially ambiguous features, we favor reversals rather than parallelisms (the ACCTRAN option) because that serves to emphasize primary homology over hypotheses of parallelism as discussed by de Pinna (1991:388). We do, however, discuss the implications of the alternative hypothesis of parallelism for such ambiguous characters as appropriate.

The meristic and morphometric features that follow were examined on the specimens that are the basis of Tables 3 to 23. These features are described in this section to facilitate the utilization of the keys and species descriptions by users with a diversity of backgrounds and interests.

MORPHOMETRICS.—Greatest body depth: Measured at the deepest point of the body, typically at the dorsal-fin origin.

Predorsal length: From the tip of the snout to the dorsal-fin origin.

Dorsal-fin base length: From the insertion of the dorsal fin to the posterior of the dorsal-fin base.

Dorsal fin to adipose fin distance: From the posterior of the dorsal-fin base to the adipose-fin insertion.

Dorsal fin to caudal fin distance: From the posterior of the dorsal-fin base to the middle of the hypural joint.

Prepelvic length: From the tip of the snout to the pelvic-fin insertion.

Preanal distance: From the tip of the snout to the anterior margin of the anus.

Snout to anal-fin insertion: From the tip of the snout to the anal-fin insertion.

Anal-fin base length: From the insertion of the anal fin to the posterior of the anal-fin base.

Caudal-peduncle length: From the posterior of the anal-fin base to the hypural joint.

Dorsal-fin length: From the anterior insertion of the dorsal fin to the tip of the longest dorsal-fin ray.

Pectoral-fin length: From the pectoral-fin insertion to the tip of the longest pectoral-fin ray.

Pelvic-fin length: From the pelvic-fin insertion to the tip of the longest pelvic-fin ray.

Least caudal-peduncle height: Minimum height of the caudal peduncle.

Head length: From the tip of the snout to the bony posterior margin of the opercle.

Snout length: From the tip of the snout to the bony anterior margin of the orbit.

Bony orbital diameter: Horizontal distance between the anterior and posterior bony margins of the orbit.

Postorbital length: From the bony posterior margin of the orbit to the posterior bony margin of the opercle.

Interorbital width: Minimum width across the interorbital region.

Mouth width: Measured between the opposite corners of the mouth.

MERISTICS.—Lateral-line scales: All pored scales along the lateral line (other than in very small specimens, all scales in series pored).

Scale rows between dorsal-fin origin and lateral line: All scales in a transverse series that starts at the dorsal-fin origin regardless of size but excludes the median dorsal scale at the dorsal-fin origin.

Scale rows between anal-fin origin and lateral line: All scales in a transverse series that starts at the anal-fin origin regardless of size, but excludes the scales that form the sheath along the anal-fin base.

Scale rows between pelvic-fin insertion and lateral line: All scales regardless of size in a transverse series between those landmarks; count starts with the scale anterior to the axillary scale.

Vertebrae: All centra in the vertebral column, including the terminal centrum and the four vertebrae incorporated into the Weberian apparatus.

Inner row teeth, upper jaw: All teeth on the left side of the upper jaw, including teeth in the process of replacement as indicated by a gap.

Inner row teeth, lower jaw: All teeth on the left side of the lower jaw, including teeth in the process of replacement as indicated by a gap.

Outer row teeth, upper jaw: All teeth on the left side of the upper jaw, including teeth in the process of replacement as indicated by a gap.

Outer row teeth, lower jaw: All teeth on the left side of the lower jaw, including teeth in the process of replacement as indicated by a gap.

Unbranched dorsal-fin rays: All unbranched rays; count includes the small bifurcate or simple procumbent spine present at the anterior of the dorsal-fin base, following Mago-Leccia (1972:38).

Branched dorsal-fin rays: All branched rays, with the two posterior dorsal-fin rays associated with separate basal pterygiophores counted as separate elements.

Branched anal-fin rays: All branched rays, with the two posterior-most rays that arise from a single basal pterygiophore counted as one element, following Fink and Weitzman (1974:2).

In the text and tables, standard length is abbreviated as SL, total length as TL, and head length as HL. Lengths of non-flexioned larvae are given as total body length, abbreviated as BL, measured from the tip of the snout to the posterior tip of the notochord.

In the text, unbranched rays are indicated by lower case Roman numbers and branched rays by Arabic numbers. Fin-ray counts are presented in the body of the text rather than in the tables in order to detail the various combinations of branched and unbranched fin-rays found in each fin across the examined samples for a species. The values of fin-ray counts for the extant holotype, lectotype, or neotype of the senior synonym for each recognized species are indicated in square brackets. Vertebral counts were taken primarily from radiographs supplemented by data from cleared and counterstained specimens. In light of the importance of counts of scales, teeth, and vertebrae in discriminating prochilodontid species, those features are presented in the tables in order to facilitate interspecific comparisons. Scale counts are particularly important in discriminating many prochilodontid species, and, as such, values for those counts are included in alternative presentations in the text and tables to highlight both the range and mode of the values in recognized species and the counts in the type series of junior synonyms.

The scales that served for the description of scale morphology in the species accounts and for the phylogenetic analysis were removed from the anterolateral portion of the body in the region dorsal to the lateral line. Scales were prepared for microscopic examination following Roberts (1993:61).

The first entry under the "Material Examined" section for each species summarizes the total number of specimens examined (with the number in parentheses being the specimens that are the basis for the meristic and morphometric data and the range of standard lengths for those specimens). In a subset of the recognized species, partial meristic data were taken from additional specimens in order to provide more comparative data for the values that serve to discriminate morphologically similar species. The number of these additional specimens is indicated after the size ranges in the introductory summary. The summary is followed by a geographically sorted list of the material examined, including collection locality, institutional abbreviation, catalog number, and number of specimens in the lot (in parentheses, the number of specimens in the lot from which counts and measurements were taken, and when available, the range of standard lengths (in mm) of all the individuals in the lots whose standard length could be accurately determined, a range that includes all specimens, not just those from which counts and measurements were taken). The number of radiographed specimens (R) in a particular lot is indicated in square brackets after the parentheses.

Type localities for nominal species in the synonymies are cited as stated in the original species description. Parenthetical information associated with locality information in synonymies either provides a translation of the original locality citation and/or supplemental information. Updated localities for Thayer Expedition collecting sites follow Higuchi (1996).

Diagnoses for most species in this paper are differential diagnoses that serve to discriminate the species from congeners rather than autapomorphies for species, the vast majority of which involve details of internal anatomy.

A few of the *Prochilodus* and *Semaprochilodus* species recognized in this paper demonstrate partial overlap in the ranges of features used to discriminate pairs of similar forms as separate species. In all such instances, the recognized species occur in separate hydrographic basins and demonstrate discrete differences in modal values for the features in question. That factor, the large-scale migrations typical of prochilodontid species, and the associated high levels of gene flow in members of the family across major river basins (Revaldaves et al., 1997, 2000; Sivasundar et al., 2001) highlight the significance of inter-drainage basin morphological differences, such as these modal values. In light of those findings, the occurrence of distinct modal differences for various features between nominal prochilodontid species in different hydrographic basins is considered to be indicative of the absence of gene flow between those populations and reflective of their distinct evolutionary histories.

The economic and ecological importance of the Prochilodontidae across vast reaches of South America is reflected in numerous citations of prochilodontids in publications that involve a spectrum of non-systematic topics (e.g., fisheries, ecology, aquaculture). Inclusion of all such citations would significantly inflate the species synonymies without contributing information pertinent to the main thrust of this paper—the resolution of the outstanding phylogenetic and species-level questions within the Prochilodontidae. The selective species synonymies herein include pertinent taxonomic papers as well as publications that deal with aspects of the life history and adaptations of diverse species. Among the latter are papers that contribute important details to this publication and/or access to the extensive literature that focuses on non-taxonomic topics that involve prochilodontids. Also included in the synonymies are citations to noteworthy non-systematic papers whose species identifications run counter to the results of this study and that are consequently deemed appropriate for comment herein. Available biological and fisheries information is briefly summarized for each species, unless such data is extensive, in which case summary reviews are cited. Citations of a species under a particular combination that are demonstrably incorrect are cited at the end of that synonymy component and are preceded by "Not."

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
CAS-SU	Stanford University Fish Collection, now at CAS
CBF	Colecion Boliviana de Fauna, La Paz
CM	Carnegie Museum (fish collections now at FMNH)
CU	Cornell University Fish Collection, Ithaca
FMNH	Field Museum of Natural History, Chicago
INHS	Illinois Natural History Survey, Champaign
INPA	Instituto Nacional de Pesquisas da Amazônia, Manaus
IU	Former Indiana University collections (now dispersed to various repositories)
LIRP	Laboratorio de Ictiologia de Ribeirão Preto, Universidade de São Paulo, Ribeirão Preto
MBUCV	Museu de Biología, Universidad Central de Venezuela, Caracas
MCP	Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre
MCZ	Museum of Comparative Zoology, Cambridge
MEPN	Museo, Escuela Politecnica Nacional, Quito
MNHN	Muséum National d'Histoire Naturelle, Paris
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	Swedish Museum of Natural History, Stockholm
SU	Stanford University, collections now at CAS
UMMZ	University of Michigan, Museum of Zoology, Ann Arbor
USNM	Former United States National Museum, collections in the NMNH.
ZMA	Instituut voor Systematiek and Populatiebiologie, Amsterdam
ZMUC	Zoologisk Museum, Copenhagen

OSTEOLOGICAL PREPARATIONS.—The following cleared and stained specimens were the basis for the observations in the phylogenetic analysis. Data from these specimens were supplemented by information in literature. The vast majority of the osteological preparations utilized in this study were cleared and counterstained for cartilage and bone using a modification of the method described by Taylor and Van Dyke (1985). Previously prepared specimens stained solely for bone with alizarin Red-S are indicated by (AR) in the listing. The number that follows the catalog number indicates the number of cleared and stained or counterstained specimens. Authorship of species and complete locality information for each lot of prochilodontids is available under the pertinent species accounts.

Prochilodontidae

Ichthyoelephas humeralis, USNM 231437 (AR), 1, 108.5 mm SL; Ecuador, no specific locality. USNM 290374, 2, 130.4–133.6 mm SL; Ecuador, Quevedo fish market.

Ichthyoelephas longirostris, MZUSP 55145, 1, 311.2 mm SL; Colombia, Río Cauca.

Prochilodus argenteus, MZUSP 42718, 2, 84.8–96.7 mm SL; Brazil, Rio São Francisco.

Prochilodus brevis, MZUSP 42717, 2, 79.0–81.9 mm SL; Brazil, Bahia, Rio Jacuípe.

Prochilodus britskii, MZUSP 38856, 1, 195.5 mm SL; Brazil, Rio Apiacá.

Prochilodus costatus, MZUSP 42687, 1, 97.3 mm SL; Brazil, Rio São Francisco. USNM 357391, 1, 103.5 mm SL; Brazil, Rio Jequitai basin.

Prochilodus hartii, MZUSP 42685, 2, 90.6–110.0 mm SL; Brazil, Bahia, Rio Jequitinhonha.

Prochilodus lacustris, MZUSP 42693, 1, 105.0 mm SL; Brazil, Maranhão, Rio Grajaú.

Prochilodus lineatus, MZUSP 42686, 2, 98.2–100.2 mm SL; Brazil, São Paulo, Rio Mogi-Guaçu.

Prochilodus magdalenae, USNM 79231, 2, 91.9–103.4 mm SL; Colombia, Calamar.

Prochilodus mariae, USNM 256959, 10, 18.5–34.5 mm SL; Venezuela, Apure, Río Apure. USNM 270243, 2, 92.6–97.1 mm SL; Venezuela, Bolivar, Río Orinoco.

Prochilodus nigricans, LIRP 1312, 5, 12.8–13.6 mm BL; Peru, Río Ucayali basin, (30 day post-spawning preflexion larvae from experimental spawning facility). MZUSP 42682, 2, 101.5–102.3 mm SL; Brazil, Pará, Rio Tocantins. USNM 241438 (AR), 1, 140.5 mm SL; Bolivia, Tumupasa. USNM 280609, 1, 78.5 mm SL; Peru, Ucayali, District Coronel Portillo, Yarinacocha.

Prochilodus reticulatus, USNM 121326, 3, 110.7–113.1 mm SL; Venezuela, Lago Maracaibo basin.

Prochilodus rubrotaeniatus, USNM 225419, 2, 89.0–100.4 mm SL; Suriname, Nickerie District, Corantijn River.

Prochilodus vimboides, MZUSP 42719, 1, 165.0 mm SL; Brazil, Bahia, Rio Jucurucu. USNM 345752, 1, 114.8 mm SL; Brazil, Minas Gerais, Rio Jequitai basin.

Semaprochilodus brama, MZUSP 42716, 2, 76.1–82.6 mm SL; Brazil, Rio Tocantins.

Semaprochilodus insignis, USNM 290148, 1, 102.5 mm SL; USNM 290149, 1, 60.8 mm SL; Brazil, Amazonas, vicinity of Manaus.

Semaprochilodus kneri, USNM 270325, 1, 99.3 mm SL; Venezuela, Amazonas, Río Orinoco, near Puerto Ayacucho.

Semaprochilodus laticeps, USNM 270239, 2, 70.0–75.0 mm SL; Venezuela, Bolivar, tributary to Río Orinoco, S of El Burro.

Semaprochilodus taeniurus, USNM 289798, 1, 78.2 mm SL; Brazil, Amazonas, near Manaus. USNM 290147, 1, 114.8 mm SL; Brazil, Amazonas, near Manaus.

Semaprochilodus varii, USNM 285719, 1, 60.3 mm SL; Suriname, Morawijne River.

Curimatidae

Curimata aspera Günther, USNM 261408, 1, 46.2 mm SL; Peru, Ucayali, at Pucallpa to Huanuco Road.

Curimata cyprinoides (Linnaeus), USNM 225619, 1, 79.2 mm SL; Suriname, Nickerie District, Makilikabroe Kreek. USNM 231433, 2, 17.1–21.4 mm SL; Suriname, Nickerie District, Corantijn River.

Curimata inornata Vari, USNM 268597, 1, 113.0 mm SL, paratype; Brazil; Pará, Rio Tapajós, São Luis.

Curimata vittata Kner, USNM 231434, 1, 53.7 mm SL; Brazil, Amazonas, Rio Negro.

Curimatella dorsalis (Eigenmann and Eigenmann), USNM 243235, 2, 51.5–53.7 mm SL; Brazil, Amazonas, Rio Solimões, Ilha Sorubim, upriver of Coari.

Curimatella immaculata (Fernández-Yépez), USNM 235524, 3, 50.2–53.0 mm SL; Venezuela, Monagas, Isla Cocos, opposite Los Castillos.

Curimatella meyeri (Steindachner), USNM 261508, 1, 100.1 mm SL; Peru, Loreto, Río Ucayali, Masisea.

Curimatopsis macrolepis Steindachner, USNM 190285, 1, 34.7 mm SL; Peru, Loreto, Iquitos. USNM 231436, 1, 59.2 mm SL; Peru, no specific locality.

Curimatopsis microlepis Eigenmann and Eigenmann, USNM 268867, 1, 75.8 mm SL; Brazil, Amazonas, Rio Solimões, near Beruri.

Cyphocharax abramoides (Kner), USNM 267953, 1, 110.3 mm SL; Brazil, Pará, Rio Xingu, Belo Monte.

Cyphocharax gillii (Eigenmann and Kennedy), USNM 232219, 1, 74.3 mm SL; Paraguay, Concepcion, 3 km NW of Lima.

Cyphocharax pantostictos Vari and Barriga, USNM 305616, 1, 66.7 mm SL; Ecuador, Napo, Río Napo, 2.7 km along river upstream of the bridge at Coca.

Potamorhina laticeps (Valenciennes), USNM 121325, 1, 129.3 mm SL; Venezuela, Zulia, Lago Maracaibo basin.

Potamorhina squamoralevis (Braga and Azpelicueta), USNM 243228, 90.2 mm SL; Brazil, Mato Grosso, Baia do Buritizal.

Psectrogaster amazonica Eigenmann and Eigenmann, USNM 261518, 1, 106.0 mm SL; Peru, Ucayali, Río Ucayali, Pucallpa.

Psectrogaster curviventris Eigenmann and Kennedy, USNM 243221, 1, 72.9 mm SL; Brazil, Mato Grosso, Baia do Buritizal.

Psectrogaster falcata (Eigenmann and Eigenmann), USNM 268041, 2, 103–110 mm SL; Brazil, Pará, Rio Tapajós, Itaituba, edge of river channel.

Pseudocurimata patiae (Eigenmann), USNM 287597, 1, 89.5 mm SL; Colombia, Departamento Narino, Río Patia, upstream of Barbacoas.

Pseudocurimata peruana (Eigenmann), USNM 285667, 1, 90.5 mm SL; Peru, Piura, Tinajones.

Steindachnerina argentea (Gill), USNM 285663, 1, 83.5 mm SL; Trinidad, northern Trinidad, Arouca River, just N of Churchill to Roosevelt Highway.

Steindachnerina conspersa (Holmberg), USNM 232224, 1, 83.2 mm SL; Paraguay, Presidente Hayes, off trans-Chaco Highway at km 50.

Steindachnerina elegans (Steindachner), USNM 297904, 2, 47.0–53.5 mm SL; Brazil, Minas Gerais, Rio Jequitinhonha, at km 205 on road between Salto da Divisa and Jacinto.

Anostomidae

Abramites hypselonotus (Günther), USNM 261479, 1, 57.5 mm SL; Peru, Ucayali, Río Ucayali, at Pucallpa.

Anostomus species, USNM 231540, 1, 81.3 mm SL; no locality data.

Leporellus pictus (Kner), USNM 302487, 1, 115 mm SL; Brazil, São Paulo, Rio Pardo, Barragem de Itaipava, near Santa Rosa de Viterbo.

Leporinus maculatus (Müller and Troschel), USNM 225397, 2, 80.3–95.1 mm SL; Suriname, Nickerie District, creek that enters Corantijn River approximately 2 km downstream of Cow Falls.

Schizodon fasciatus Agassiz, USNM 280739, 2, 88.5–106.1 mm SL; Peru, Loreto, District Coronel Portillo, Yarinacocha.

Chilodontidae

Caenotropus maculosus (Eigenmann), USNM 231545, 2, 42.7–46.3 mm SL; Guyana.

Caenotropus mestomorgmatos Vari, Castro, and Raredon, USNM 322557, 1 paratype, 102 mm SL; Venezuela, Amazonas, Río Iguapo (tributary of Río Orinoco), approximately 1 hour by boat upstream of its mouth.

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

Chilodus punctatus Müller and Troschel, USNM 280444, 2, 55.7–68.0 mm SL; Peru, Loreto, Quebrada Corrientillo, at Corrientillo, on road that runs W from Iquitos to Río Nanay.

Crenuchidae

Ammocryptocharax elegans Weitzman and Kanazawa, USNM 210691, 3, 34.2–39.9 mm SL; Brazil, region along Brazil-Bolivian border between Guajara-Mirim and Mato-Grosso.

Parodontidae

Parodon suborbitalis Valenciennes, USNM 231552, 2, 55.0–58.1 mm SL; Colombia, Río Salado.

Saccodon dariensis (Meek and Hildebrand), USNM 208505, 1, 73.3 mm SL; Panama, Río Membrillo.

TERMINOLOGY.—Some authors (e.g., Géry, 1977:210, footnote) have cited the family Prochilodontidae as the Prochilodidae, assuming that the root for the familial name is "Prochilod." As discussed by Steyskal (1980:173), "names in -*odus* are usually from Greek *odous* 'tooth,' are of masculine gender, and have a stem in *-odont-*." Consequently, the proper form of the family name is Prochilodontidae.

The family Prochilodontidae of this study was recognized by Nelson (1994) as the subfamily Prochilodontinae within the family Curimatidae, a shift from the general practice that commenced with Greenwood et al. (1966). Neither Nelson (1994) nor subsequently Eschmeyer (1998) detailed the advantage of a shift from the commonly utilized family level for the group. Furthermore, such a change is unnecessary both within the framework of the phylogenetic hypotheses advanced by Vari (1983, 1989a), Ortí (1997), Ortí and Meyer (1997), and this study. Indeed, the recognition of a subfamily Prochilodontinae within an expanded Curimatidae has engendered confusion because it runs counter to the usual practice among researchers who actively publish on the taxonomy, life history, and fisheries of these groups (e.g., CLOFFSCA, 2003) and who recognize separate families Prochilodontidae and Curimatidae. We consequently follow the practice most common in the primary taxonomic literature and recognize the group treated herein as a family, the Prochilodontidae.

Osteological terminology used herein is that proposed by Weitzman (1962) with the following modifications discussed by Vari (1989a). Vomer is substituted for prevomer and intercalar for opisthotic, as in most recent publications that deal with characiforms. The use of epioccipital rather than epiotic follows Patterson (1975), and the use of angulo-articular for articular and retroarticular instead of angular is that of Nelson (1973). Use of posterior ceratohyal for epihyal and anterior ceratohyal for ceratohyal follows Nelson (1969), and mesethmoid rather than ethmoid follows Fink and Fink (1981).

The concepts of characiform families in this paper are those of Greenwood et al. (1966) with the following modifications. The members of the family Ichthyboridae of Greenwood et al. (1966) form a subunit of the Distichodontidae following Vari (1979), and the Cynodontidae of those authors is recognized as the subfamily Cynodontinae within a more encompassing Cynodontidae in keeping with the results of Howes (1976), Lucena and Menezes (1998), and Toledo-Piza (2000). *Anodus* and *Eigenmannina* Fowler, assigned to the Curimatidae by Greenwood et al. (1966), are instead placed in the Hemiodontidae as justified by Langeani (1998). Old World taxa assigned to the Characidae according to Greenwood et al. (1966) are referred to herein as the Alestidae as proposed by Buckup (1998) and discussed by Vari and Ortega (2000).

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Character Descriptions and Analysis

Our paramount aim in this section is the development of an explicit hypothesis of the phylogenetic relationships within the family Prochilodontidae, with a secondary aim of testing the hypothesized monophyly of that family as first formally proposed by Vari (1983).

The four hypothesized synapomorphies for the clade formed by the Prochilodontidae, Curimatidae, Anostomidae, and Chilodontidae were discussed in detail by Vari (1983) and are not considered again herein. An additional (fifth) synapomorphy, discovered during the course of this study, is proposed and discussed for that clade (see "Monophyly of the Prochilodontidae, Curimatidae, Anostomidae, and Chilodontidae Clade"). The hypothesis of a sister-group relationship between the Prochilodontidae and Curimatidae by Vari (1983) was based upon the examination of character systems in a subset of the species in the Prochilodontidae recognized as valid herein. These characters are only briefly summarized herein, but they were confirmed as present in all recognized species of the Prochilodontidae during this study. Synapomorphies for the clade formed by the Prochilodontidae and Curimatidae are, however, neither included in Table 2 nor in the phylogenetic analysis. More extensive discussions of synapomorphies for the Prochilodontidae plus Curimatidae, their polarity, and taxonomic distribution can be found in Vari (1983).

Analyzed characters that demonstrate phylogenetically informative variation are discussed within the context of outgroup comparisons that permit the polarization of the feature in question. For the purposes of polarization of the discussed characters, the first outgroup is the Curimatidae that was hypothesized to be the sister group to the Prochilodontidae on the basis of morphological (Vari, 1983, 1989a) and molecular (Ortí, 1997; Ortí and Meyer, 1997) data. The second outgroup is the lineage formed by the Anostomidae plus Chilodontidae that together form the sister group to the clade formed by the Prochilodontidae plus Curimatidae (Vari, 1983, and evidence herein). A number of body systems (e.g., dentition) are highly modified in some, or all, of the immediate successive outgroups to the Prochilodontidae. These modifications render these immediate outgroups inappropriate as the basis for polarization of features in such body systems and necessitated comparisons to characiform outgroups outside of the clade formed by those four families, with a focus on taxa towards the base of the phylogeny of the Characiformes following Buckup (1998). Meristic features yielded few discrete polarizable characters as a consequence of the similarity of those attributes across the Prochilodontidae and the consequent intraspecific overlap in those features. Characters utilized in the phylogenetic analysis are those demonstrating discrete states either within the Prochilodontidae or between the members of that family and outgroups. The continuum in the variation of other features in several body systems makes it impossible to unambiguously code the state for any particular species, so such variation was not incorporated into the analysis.

Vari (1983) proposed a series of hypothesized synapomorphies for members of the Prochilodontidae, which consisted of a subset of the species recognized in the family herein. These putative synapomorphies have been reevaluated in this study for all species of the Prochilodontidae. In some instances, these more encompassing comparisons revealed previously undetected variation in a character system and either lead to a redefinition of the feature, or its subdivision into more than one character. The 18 synapomorphies for the Prochilodontidae proposed by Vari (1983) are supplemented by an additional 40 synapomorphies for that family discovered during this analysis.

In the sections that follow, we discuss characters hypothesized to be synapomorphic for assemblages that range from the clade that consists of the four families (Prochilodontidae, Curimatidae, Anostomidae, Chilodontidae) to species pairs within the Prochilodontidae. Only features pertinent to the monophyly of the Prochilodontidae or informative as to phylogenetic relationships within that family are assigned character numbers and are included in Table 2. Each phylogenetically informative feature is first described in detail and outgroup conditions are discussed. The discussion is followed by the character letter (synapomorphies for the clades that consist first of the Anostomidae, Chilodontidae, Curimatidae, and Prochilodontidae and secondly of the Curimatidae and Prochilodontidae) or number (synapomorphies for the Prochilodontidae and clades within that family), a summary description of the structure(s) of interest, and descriptions of the different character states.

BRANCHIAL ARCHES

Previous studies (Vari, 1983, 1989a) demonstrated that the bones, cartilages, muscles, and connective tissues of the branchial arches are a treasure trove of phylogenetically informa-

TABLE 2.—Character matrix of 125 characters for the species of Prochilodontidae. Character numbers correspond to those in the text.

Taxon	Character												
	1–10	11–20	21–30	31–40	41–50	51–60	61–70	71–80	81–90	91–100	101–110	111–120	121–124
Outgroup	00000?0000	0000000000	0000000000	00000000?0	0?00000?00	00?0000000	0000000000	0?0000000?	0000000000	00000?0?00	?000000000	0000000000	?000
Prochilodus													
argenteus	1110111101	1111001111	1111110111	1001111101	1000001111	1101011111	1120011200	0100101011	1110101111	0110111101	0001000001	1110010001	2010
brevis	1110111101	1111001111	1111110111	1001111101	1000001111	1101011111	1120011200	0100101011	1110101111	0110111101	0001000001	1110010011	2010
britskii	1110111101	1111001111	1111110111	1001111101	1000001111	1101011111	1120011200	0100101011	1110101111	0110111101	0001000001	1110000001	2010
costatus	1110111101	1111001111	1111110111	1001111101	1000001111	1101011111	1120011200	0100101011	1110101111	0110111101	0001000001	1110010001	2010
hartii	1110111101	1111001111	1111110111	1001111101	1000001111	1101011111	1120011200	0100101011	1110101111	0110111101	0001000001	1110010001	2010
lacustris	1110111101	1111001111	1111110111	1001111101	1000001111	1101011111	1120011200	0100101011	1110101111	0110111101	0001000001	1110010011	2010
lineatus	1110111101	1111001111	1111110111	1001111101	1000001111	1101011111	1120011200	0100101011	1110101111	0110111101	0001000001	1110010001	2010
magdalenae	1110111101	1111001111	1111110111	1001111101	1000001111	1101011111	1120011200	0100101011	1110101111	0110111101	0001000001	1110000001	2010
mariae	1110111101	1111001111	1111110111	1001111101	1000001111	1101011111	1120011200	0100101011	1110101111	0110111101	0001000001	1110010011	2010
nigricans	1110111101	1111001111	1111110111	1001111101	1000001111	1101011111	1120011200	0100101011	1110101111	0110111101	0001000001	1110010011	2011
reticulatus	1110111101	1111001111	1111110111	1001111101	1000001111	1101011111	1120011200	0100101011	1110101111	0110111101	0001000001	1110000001	2010
rubrotaeniatus	1110111101	1111001111	1111110111	1001111101	1000001111	1101011111	1120011200	0100101011	1110101111	0110111101	0001000001	1110010011	2011
vimboides	1110111101	1111001111	1111110111	1001111101	1000001111	1101011111	1120011200	0100101011	1101011111	0110111101	0001000001	1110000001	2010
Semaprochilodus													
brama	0100100001	0101001111	1111110111	1011111111	1011111111	1100011110	1110011110	0200011012	1110100101	0110111101	0011110011	1102011101	2100
insignis	0100100011	0101001111	1111110111	1011111111	1021111111	1100011110	1110011111	0200011012	1110100101	0110111111	0011110011	1101011101	2100
kneri	0100100011	0101001111	1111110111	1011111111	1021111111	1111011111	1110011111	0200011012	1110100101	0110111111	0011110011	1101011101	2100
laticeps	0100100001	0101001111	1111110111	1011111111	1011111111	1100011110	1110011110	0200011012	1110100101	0110111101	0011110011	1102011101	2100
taeniurus	0100100011	0101001111	1111110111	1011111111	1011111111	1100011110	1110011111	0200011012	1110100101	0110111101	0011110011	1101011101	2100
varii	0100100001	0101001111	1111110111	1011111111	1011111111	1100011110	1110011110	0200011012	1110100101	0110111101	0011110011	1102011101	2100
Ichthyoelephas													
humeralis	0??1100000	0101111111	1211111111	1101111111	1102102111	1110111110	1111121100	1111001111	1121110101	1111121201	1111201101	1100100001	1100
longirostris	0??1100000	0101111111	1211111111	1101111111	1102102111	1110111110	1111121100	1111001111	1121110101	1111121201	1111201101	1100100001	1100

tive characters both for the clade formed of the Prochilodontidae and Curimatidae and at less encompassing taxonomic levels. These systems proved equally productive for the question of the monophyly of the Prochilodontidae and for the partial resolution of intrafamilial phylogenetic relationships.

The discussion of a synapomorphy of the gill filaments common to all gill arches is followed by remarks on phylogenetically informative features in the branchial arches, which are subdivided between dorsal and ventral components of the gill arches. Within those major divisions, the discussion is arranged in subunits that usually consist of components of the individual gill arches.

Gill Filaments

Proximate outgroups to the Prochilodontidae (Curimatidae, Anostomidae, Chilodontidae) have completely unossified gill filaments, a condition also universal in the prochilodontid genera *Ichthyoelephas* and *Semaprochilodus*. Cleared and stained specimens of species of *Prochilodus*, in contrast, have the forked basal portion of all gill filaments ossified, albeit with variation in the degree of ossification within and between gill arches. Filaments on the dorsal limb of an arch have an ossification that encompasses both the forked basal portion of the filament and the base of the main shaft of each element. The degree of ossification of the shaft of the filaments progressively decreases anteriorly on the lower limb of each arch, and at least in the largest examined cleared and stained specimens of *Prochilodus*, the ossification on the medial-most filaments remains limited to the basal forked portion of the filament. Given the ontogenetic progression in the extent of the ossification of the filaments, it is likely that a greater proportion of each filament is ossified in specimens of larger sizes than those cleared and stained for this study. The degree of ossification of the gill filaments on the outer face of a particular gill arch is greater than those of the filaments on the corresponding inner face of the comparable region of that arch. In light of the absence of such gill filament ossifications in other examined characiforms, the presence of those structures in the species of *Prochilodus* is hypothesized to be a synapomorphy for the members of that genus.

The ossified basal portions of the filaments were apparently interpreted by Oliveros and Occhi (1972:132, fig. 7) as structures ("Processos digitiformes") independent of the gill filaments in *Prochilodus lineatus* (the *P. platensis* of those authors). Our observations indicate that the basal ossified portions and the main shaft of the filament in that species are rather continuously ossified, the general condition for other *Prochilodus* species. The difficulty in observing the continuity of these structures in specimens that have not been cleared and stained may account for the identification of the ossified basal portions of the gill filaments as separate elements by Oliveros and Occhi (1992).

CHARACTER 1. Condition of the basal portions of the gill filaments. State 0: Unossified; State 1: Ossified.

Dorsal Portions of Branchial Arches

FIRST INFRAPHARYNGOBRANCHIAL.—The first infrapharyngobranchial of characiforms is almost always a dorsally to dorsolaterally directed bone positioned dorsal to the upper surface of the anterior portion of the first epibranchial (Figure 1A). Species of *Prochilodus* and *Semaprochilodus* have the basal portion of the first infrapharyngobranchial significantly widened along its area of contact with the first epibranchial. As a consequence of this expansion of the first infrapharyngobranchial, the ventral portion of that ossification in *Prochilodus* and *Semaprochilodus* contacts the cartilages that cap the anterior portions of the first and second epibranchials. Proximate outgroups to the Prochilodontidae lack contact between the first infrapharyngobranchial and the second epibranchial, and such a juxtaposition of those elements in *Prochilodus* and *Semaprochilodus* is hypothesized to be derived. Given the absence of a first epibranchial in *Ichthyoelephas* (see discussion below), the condition of the basal portion of that ossification in the species of that genus is coded as unknown in this analysis. The overall most parsimonious hypothesis of relationships arrived at in this study indicates that a first infrapharyngobranchial in contact with the second epibranchial is a derived feature synapomorphic for the Prochilodontidae, albeit with a secondary loss of the character (and first infrapharyngobranchial) in the species of *Ichthyoelephas* (see below).

CHARACTER 2. Relative width of basal portion of first infrapharyngobranchial. State 0: Not expanded and not in contact with second epibranchial; State 1: Expanded and in contact with second epibranchial.

The overall morphology of the first infrapharyngobranchial in the species of *Prochilodus* is unique among examined taxa. In *Prochilodus*, the dorsal process of the first infrapharyngobranchial has a distinctly more lateral orientation than it does in other examined characiforms, and the entire ventral portion of the bone is distinctly elongate transversely (Figure 1B,C). Neither *Semaprochilodus* nor the species of the Curimatidae, the proximate outgroup to the Prochilodontidae, demonstrate such a transverse elongation of the first infrapharyngobranchial. (The ossification is absent in *Ichthyoelephas*, and the character is consequently coded as unknown for the species of that genus in this analysis.) Neither does the form of the first infrapharyngobranchial characteristic of *Prochilodus* species occur in the secondary outgroup (Anostomidae plus Chilodontidae). The form of the first infrapharyngobranchial in *Prochilodus* is, thus, considered derived.

CHARACTER 3. Form of the first infrapharyngobranchial. State 0: Approximately straight or triangular; State 1: Distinctly transversely elongate.

As noted, an ossified first infrapharyngobranchial is absent in all examined cleared and stained specimens of *Ichthyoele-*

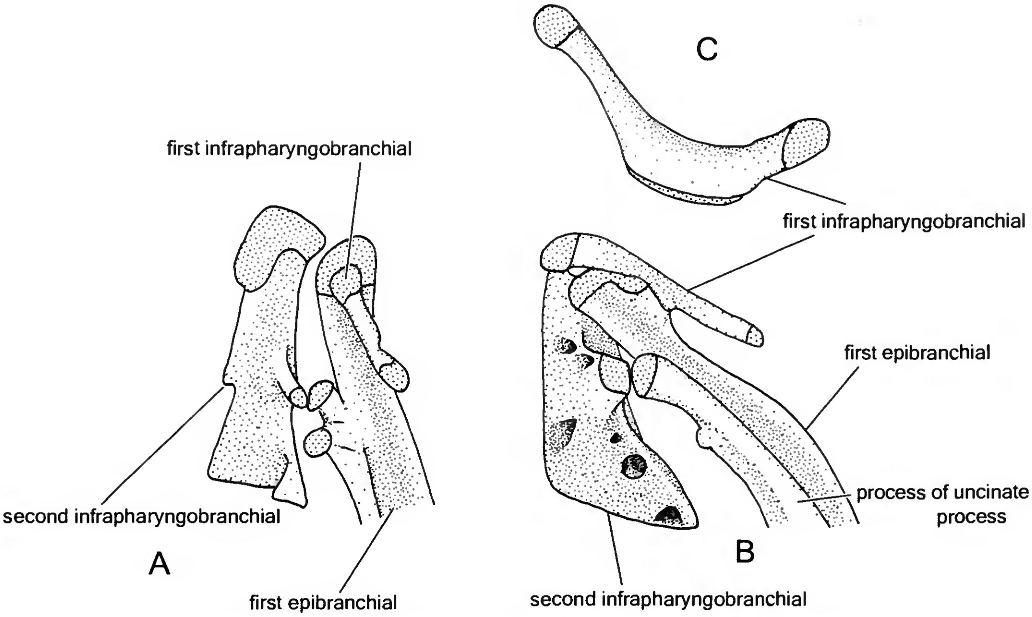


FIGURE 1.—Right first infrapharyngobranchial and associated elements: A, *Potamorhina laticeps*, USNM 121325; B,C, *Prochilodus nigricans*, MZUSP 42682. Structures in A and B are shown in dorsal view with anterior at top and medial to left; C is shown in anterior view with dorsal at top and medial to right. (Dense patterned stippling represents cartilage.)

phas, although members of the genus retain a cartilage in the region primitively occupied by the first infrapharyngobranchial that may represent a remnant of that ossification. All components of the proximate outgroups to Prochilodontidae (Curimatidae, Anostomidae, Chilodontidae) retain an ossified first infrapharyngobranchial except for three species of *Curimata* (*C. cisandina, C. inornata, C. roseni*) that constitute a clade that is deeply nested within the phylogeny of the Curimatidae (Vari, 1989a:26; 1989b:7). Given the presence of the first infrapharyngobranchial in the examined members of the secondary outgroup (Anostomidae plus Chilodontidae), in all but three of the almost 100 species in first outgroup (Curimatidae), including the basal curimatid lineages *Curimatopsis* and *Potamorhina* (Vari, 1989a, fig. 44), and in basal clades within *Curimata* (Vari, 1989b, fig. 14), the possession of an ossified first infrapharyngobranchial is considered to be the plesiomorphic condition within the Prochilodontidae. The lack of an ossified first infrapharyngobranchial in the species of *Ichthyoelephas* is, thus, hypothesized to be derived, albeit homoplastically present within a minor clade of the first outgroup, the Curimatidae.

CHARACTER 4. Ossified first infrapharyngobranchial. State 0: Present; State 1: Absent

FIRST EPIBRANCHIAL.—All members of the Prochilodontidae have a posterolaterally oriented process that arises from the base of the uncinate process of the first epibranchial (Figure 1B) and that extends into the trough-like portion of the ossification that extends along much of the length of the bone. Such an elaboration of the first epibranchial is absent in examined outgroup characiforms. Thus, the possession of this process is hypothesized to be a synapomorphy for the species of the Prochilodontidae.

CHARACTER 5. Posterolaterally oriented process that arises from base of uncinate process of first epibranchial. State 0: Absent; State 1: Present.

The posteriorly oriented process that arises from the base of the uncinate process of the first epibranchial is moderately developed in the species of *Ichthyoelephas* and *Semaprochilodus* but is markedly expanded into a more laterally directed and horizontally aligned, flange-like process in the species of *Prochilodus*. The absence of this process in outgroup characiforms makes it impossible to polarize the two conditions of the structure (moderately versus well developed) present in prochilodontid subgroups, but the well-developed flange is optimized as a synapomorphy for the species of *Prochilodus* under the overall most parsimonious hypothesis of relationships arrived at in this study (see "Phylogenetic Reconstruction").

CHARACTER 6. Degree of development of posterolaterally oriented process that arises from base of uncinate process of first epibranchial. State 0: Moderately developed; State 1: Highly developed into laterally directed, horizontally aligned, flange-like process.

FIRST THROUGH THIRD EPIBRANCHIALS.—Characiforms typically have a smooth anterodorsal margin on the first through third epibranchials, the condition found in proximate

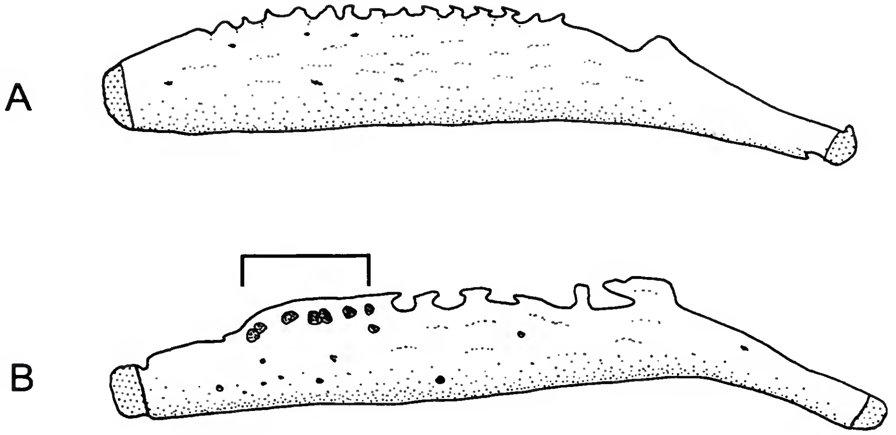


FIGURE 2.—Right first epibranchial: A, *Prochilodus rubrotaeniatus*, USNM 225419, showing serrations along dorsal margin of anterior surface; B, *Prochilodus britskii*, MZUSP 38856, showing serrations and porthole-like (limits indicated by bracket) along dorsal margin of anterior surface. Dorsal at top and medial at right, with drawings not to scale. (Dense patterned stippling represents cartilage.)

outgroups to the Prochilodontidae and within that family in *Ichthyoelephas* and *Semaprochilodus*. The species of *Prochilodus* instead posses a series of serrae of varying form situated along the anterodorsal margins of the first through third epibranchials (Figure 2A,B). These serrae are situated proximate to the ossified basal portions of the gill filaments characteristic of these genera. Comparisons of cleared and stained *Prochilodus* specimens of different sizes demonstrated a proportional enlargement of the distal region of the serrae with increasing body size; this trend culminates in an ontogenetic coalescence of the distal portions of adjoining serrae in larger individuals. In the larger size cleared and stained specimens examined, this fusion results in the formation of a series of porthole-like openings along at least portions of the anteroventral margins of the first through third epibranchials (Figure 2B). Given their unique nature among examined characiforms, the serrations that are present in all examined specimens and the porthole-like openings that apparently develop from them ontogenetically are hypothesized to be a synapomorphy for the species of *Prochilodus*.

CHARACTER 7. Form of anterodorsal margins of first through third epibranchials. State 0: Approximately smooth; State 1: With series of serrae at various body sizes and with serrae and porthole-like openings in larger specimens.

SECOND EPIBRANCHIAL.—Two subunits of the Prochilodontidae demonstrate phylogenetically informative modifications of the uncinate process of the second epibranchial. In all species of *Prochilodus*, the uncinate process has a distinct ridge-like process that extends posterolaterally along its anterior surface. The degree of development of the process differs among the species of the genus, with the variation forming a continuum that renders it impossible to parse the different morphologies into discrete characters. A comparable process on the second epibranchial is, however, absent both in *Ichthyoelephas* and *Semaprochilodus* in the Prochilodontidae and also among proximate outgroups to that family. The possession of the process, regardless of its degree of development, is consequently hypothesized to be a synapomorphy for the species of *Prochilodus*.

CHARACTER 8. Form of anterior surface of uncinate process of second epibranchial. State 0: Unelaborated; State 1: With distinct ridge-like process.

Three species of *Semaprochilodus* have the articular surface of the uncinate process on the second epibranchial vertically expanded, with a consequent moderate (*S. kneri, S. taeniurus*) or pronounced elongation (*S. insignis*) of the cartilage that caps the uncinate process. In the case of *S. insignis*, the elongation of the uncinate process is pronounced to such a degree that the cartilage that caps the process becomes divided into two portions. The elongation of the articular surface of the uncinate process to some degree is a derived condition synapomorphic for *S. kneri, S. taeniurus*, and *S. insignis*. The subdivision of the cartilage cap is, in turn, an autapomorphy for *S. insignis*.

CHARACTER 9. Cartilage-capped articular surface of uncinate process on second epibranchial. State 0: Not vertically expanded; State 1: Vertically expanded.

THIRD INFRAPHARYNGOBRANCHIAL.—The restructuring of the posterolateral portion of the third infrapharyngobranchial from the flat structure typical for characiforms into a distinct dorsally aligned flange that is visible in a medial view of the gill arches was proposed by Vari (1989:23-24) as a derived feature synapomorphic for the Prochilodontidae plus Curimatidae. This hypothesis was based upon the examination of a subset of the species in the Prochilodontidae. The broader comparative studies in this analysis have confirmed that this modification of the third infrapharyngobranchial is universal across the

Prochilodontidae and supported the proposed hypothesis of the derived nature of the feature for that family and the Curimatidae.

THIRD EPIBRANCHIAL.—The third epibranchial has a lateral or slightly anterolateral orientation among many outgroups to the Prochilodontidae and Curimatidae. In light of that observation and based upon a study of a subset of species in the Prochilodontidae, Vari (1989a:22) proposed that the expansion and restructuring of the uncinate process of the third epibranchial into an anterior process that overlies the articulation between the third infrapharyngobranchial and the third epibranchial was a synapomorphy for the Prochilodontidae plus Curimatidae. The more encompassing examination of all species of the Prochilodontidae in this study has confirmed the universal presence of that feature across that family, and the additional outgroup comparisons also have supported the hypothesis of the derived nature of this modification of the third epibranchial.

A subdivision of the anterior articular surface of the third epibranchial and the associated expansion and reorientation of the medial portion of the articulation into a medially directed, ossified process that extends along a corresponding groove on the anterodorsal portion of the fourth infrapharyngobranchial was proposed by Vari (1989a:23) as a synapomorphy for the clade that consists of the Prochilodontidae plus Curimatidae, again based upon a survey of a subset of the species in the Prochilodontidae. That feature was found in this study to be universal among all species of the Prochilodontidae, and additional outgroup comparisons support the hypothesis of its derived nature within the Characiformes.

FOURTH UPPER PHARYNGEAL TOOTH PLATE.—Vari (1983: 17–18) hypothesized that the restructuring of the plesiomorphously flat fourth upper pharyngeal tooth plate into a curved ossification that wraps around the ventral, lateral, and medial surfaces of the fourth infrapharyngobranchial (see Vari, 1983, figs. 16, 17) was a synapomorphy for the Prochilodontidae plus Curimatidae. More exhaustive comparisons in this study that involve all species of the Prochilodontidae confirm the generality of such a restructured fourth epibranchial tooth plate across that family. Outgroup comparisons also are consistent with the hypothesis that the possession of this form of the fourth epibranchial tooth plate is a synapomorphy for the clade that consists of the Prochilodontidae plus Curimatidae.

These more encompassing intrafamilial comparisons, however, also have revealed that the degree of development of the fourth upper pharyngeal tooth plate in the species of *Prochilodus* and *Semaprochilodus* is greater than that present in *Ichthyoelephas* or the members of the Curimatidae. In the Curimatidae, the fourth upper pharyngeal tooth plate extends dorsally to cover only the medial surface of the cartilaginous fourth infrapharyngobranchial. Alternatively, in the species of *Prochilodus* and *Semaprochilodus* the more extensive medial portion of the highly modified fourth upper pharyngeal tooth plate extends onto the dorsal and in some instances onto the anterior surfaces of the fourth infrapharyngobranchial. At its maximum this dorsal extension of the fourth upper pharyngeal tooth plate continues around the cartilaginous fifth infrapharyngobranchial to contact, but not fuse with, the anterodorsal margin of that tooth plate. In such instances, at least the mid-region of the cartilaginous fourth infrapharyngobranchial is completely encircled by the fourth upper pharyngeal tooth plate. Under the most parsimonious hypothesis of phylogenetic relationships, this elaboration of the fourth upper pharyngeal tooth plate beyond the degree of development present in the Curimatidae is considered to be a synapomorphy for the Prochilodontidae, albeit with a secondary reduction in *Ichthyoelephas*. The hypothesis that the condition of the fourth upper pharyngeal tooth plate in *Ichthyoelephas* represents a secondary reduction relative to the morphology present in more encompassing clades is supported by the observation that the members of the Curimatidae, the sister group to the Prochilodontidae, also possess a more extensive development of the fourth upper pharyngeal tooth plate along the medial surface of the fourth infrapharyngobranchial than is present in *Ichthyoelephas*. Given the lack of a comparable expansion of the fourth infrapharyngobranchial in other characiforms, the more extensive expansion of the medial portion of the fourth upper pharyngeal tooth plate along the medial surface of the fourth infrapharyngobranchial is hypothesized to be derived at the level of the ancestor of the Prochilodontidae plus Curimatidae, with the condition in *Ichthyoelephas* a secondary reduction.

CHARACTER 10. Degree of development of the primitively medial portion of the fourth upper pharyngeal tooth plate. State 0: Fourth upper pharyngeal tooth plate limited to the ventral and posterior surfaces of fourth infrapharyngobranchial; State 1: Fourth upper pharyngeal tooth plate covers ventral, posterior, dorsal, and sometimes anterior surfaces of fourth infrapharyngobranchial.

FOURTH UPPER PHARYNGEAL TOOTH PLATE AND FOURTH INFRAPHARYNGOBRANCHIAL.—In his analysis of the relationships of the Prochilodontidae and Curimatidae, Vari (1989a:21) proposed that the constriction of the complex formed by the fourth infrapharyngobranchial and the fourth upper pharyngeal tooth plate, as reflected in the convex lateral margin to those conjoined elements, was a synapomorphy for the two families (Vari, 1983, 1989a). This hypothesis was based upon a survey of a subset of prochilodontid species. More encompassing surveys across the Prochilodontidae than were undertaken in that earlier study confirmed the universal occurrence in that family of this modification of the fourth infrapharyngobranchial and fourth upper pharyngeal tooth plate. The feature is hypothesized herein as a synapomorphy for the Prochilodontidae plus Curimatidae, a finding in keeping with the hypothesis advanced by Vari (1983).

FOURTH EPIBRANCHIAL.—Vari (1983:20; 1989a:19, figs. 5–11) proposed that the reorientation of the dorsal process of the fourth epibranchial from the dorsal orientation that it assumes in other characiforms (e.g., *Brycon meeki,* Vari, 1983, fig. 15a)

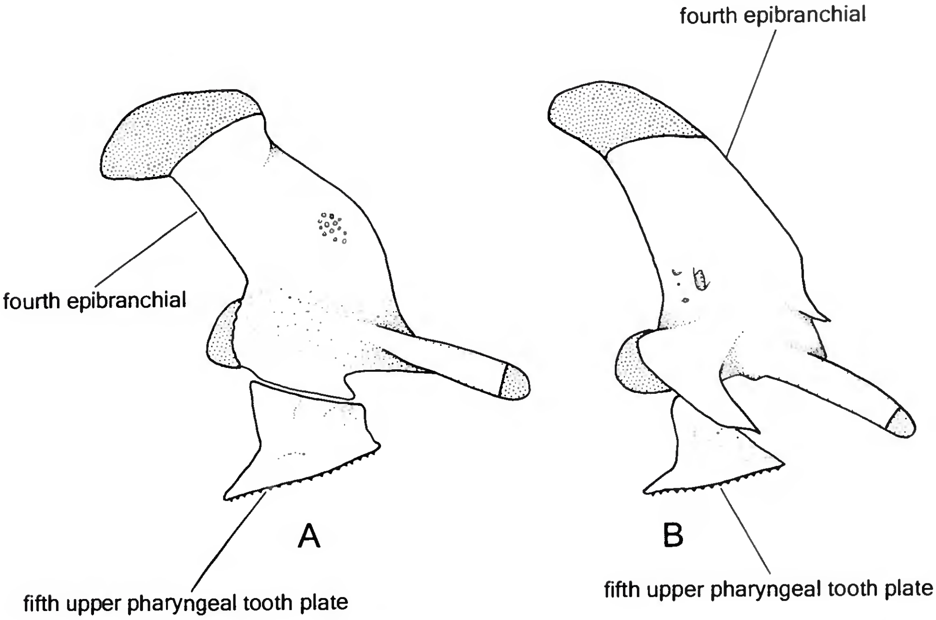


FIGURE 3.—Medial view of right fourth epibranchial and fifth upper pharyngeal tooth plate: A, *Semaprochilodus brama*, MZUSP 21256; B, *Prochilodus nigricans*, MZUSP 32682, showing more highly developed ventral process of the fourth epibranchial in *Prochilodus* species. (Dense patterned stippling represents cartilage.)

into a more anterior orientation, with the resultant extension of that process over the dorsal portion of the fourth infrapharyngobranchial, was a synapomorphy for the clade that consists of the Curimatidae (see Vari, 1989a, figs. 8–11) plus Prochilodontidae (Figure 3A,B). Our analysis confirms that the possession of this form of the dorsal process of the fourth epibranchial is universal within the Prochilodontidae. The broader outgroup comparisons herein confirm that the reorientation of the fourth epibranchial is derived and synapomorphic for the clade formed by the Curimatidae plus Prochilodontidae.

Modifications of the fourth epibranchial also are phylogenetically informative within the Prochilodontidae. In *Ichthyoelephas* (see Vari, 1983, fig. 15c) and *Semaprochilodus*, the ventral portion of the fourth epibranchial that articulates with the dorsal portion of the fifth upper pharyngeal tooth plate, although proportionally larger than that present in many characiforms (e.g., *Brycon*, Vari, 1983, fig. 15a), nonetheless approximates the condition present in the Curimatidae (e.g., *Curimata*, Vari, 1983, fig. 15b). In the species of *Prochilodus*, the ventral portion of the fourth epibranchial is expanded into a slightly medially curving, proportionally more posteriorly elongate process with an expanded articular surface that contacts the dorsal surface of the highly modified fifth upper pharyngeal tooth plate (Figure 3B, see also Vari, 1989a, fig. 6, VAP). In light of its unique nature among examined characiforms, this elaboration of the ventral portion of the fourth epibranchial is hypothesized to be a synapomorphy for the species of *Prochilodus*.

CHARACTER 11. Degree of development of the ventral portion of the fourth epibranchial. State 0: Moderately developed; State 1: Highly developed into slightly medially curving, proportionally more posteriorly elongate process.

FIFTH EPIBRANCHIAL.—Vari (1983:20, fig. 15; 1989a:51, figs. 5, 6, 8–11) hypothesized that the anterodorsal expansion of the cartilaginous fifth epibranchial and the attachment of that enlarged cartilage to the posterodorsal margin of the fourth epibranchial with the consequent encirclement of the fifth efferent branchial artery by these structures was synapomorphic for the Prochilodontidae plus Curimatidae. Broader examinations within, and outside of, the Prochilodontidae in this study confirm both the occurrence of these modifications of the fourth epibranchial in all members of that family and their unique nature among examined characiforms. This finding is congruent with the previous hypothesis of this modification as a synapomorphy for the Curimatidae plus Prochilodontidae.

FIFTH UPPER PHARYNGEAL TOOTH PLATE.—Vari (1983:19) cited the highly modified, transversely compressed, fifth upper pharyngeal tooth plate (see Figure 3 for *Semaprochilodus* and *Prochilodus* and Roberts, 1973b, fig. 33 for *Ichthyoelephas*) and the associated mobility of that ossification with respect to the ventral surface of the fourth epibranchial as a synapomorphy for all of the examined species of the Prochilodontidae based upon an examination of a subset of the species in that family. The examination of all species in the Prochilodontidae and the associated outgroup comparisons in this study confirm that conclusion. Further information on this character is available in Vari (1983:19).

CHARACTER 12. Form of fifth upper tooth plate and its association with fourth epibranchial. State 0: Not transversely compressed and with little or no mobility relative to fourth epibranchial; State 1: Transversely compressed and with distinct mobility relative to fourth epibranchial.

The ontogenetic reduction or loss of the dentition associated with the ventral surface of the fifth upper pharyngeal tooth plate was hypothesized by Vari (1983:19) to be a synapomorphy for the clade formed by the Prochilodontidae (Figure 3) plus Curimatidae (see Vari, 1989a, figs. 7–11). Examination of smaller individuals of the Prochilodontidae than were available in that earlier study (*Prochilodus mariae,* USNM 256959, 18.5–34.5 mm SL; *P. nigricans,* LIRP 1312, 12.8–13.6 mm BL) along with subsequently published information (Rossi, 1993:163, fig. 3) indicate that the proportionally large dentition associated with this tooth plate in smaller prochilodontid specimens undergoes a progressive ontogenetic reduction. In *P. lineatus,* the timing of this reduction in the extent of the dentition on the fifth upper pharyngeal tooth plate is correlated with a change from the zooplanktivorous diet of the larvae to the detritivorous diet of larger individuals (Rossi, 1993:164). Comparable shifts in diet also have been reported for other *Prochilodus* species (Godoy, 1975; Rosa and Schubart, 1945) and for *Semaprochilodus insignis* (Araújo-Lima and Hardy, 1987). Although ontogenetic changes in diet have not been critically examined in other prochilodontid species, it is reasonable to assume that such a dietary shift is general across the family, given that all prochilodontids are detritivorous as adults. Such a loss of the dentition associated with the fifth upper pharyngeal tooth plate is considered to be derived, given the continued presence of these teeth throughout ontogeny in both proximate outgroups to the Prochilodontidae and Curimatidae (Anostomidae, Chilodontidae) and other lineages within the Characiformes. These results are congruent with the hypothesis put forward by Vari (1983) under which the absence, or near absence, of dentition in the fifth upper pharyngeal tooth plate is a synapomorphy for the Prochilodontidae plus Curimatidae.

EPIBRANCHIAL ORGAN.—The possession of large, longitudinally aligned, sac-like epibranchial organs that extend dorsal of the posteromedial elements of the dorsal portions of the gill arches (see Menin and Mimura, 1991, fig. 1) and that have both longitudinal and circular muscles in their walls was proposed by Vari (1983:21–24) as a synapomorphy for the clade that consists of the Prochilodontidae plus Curimatidae. The more encompassing survey of the Prochilodontidae in this study confirms the presence of such a form of epibranchial organ in all members of the family. Given the unique form of the epibranchial organ in these families among characiforms, we follow Vari (1983, 1989a) and consider the possession of an epibranchial organ with the cited characteristics to be a synapomorphy for the clade formed by the Prochilodontidae and Curimatidae.

Ventral Portions of Branchial Arches

FIRST BASIBRANCHIAL.—In his analysis of modifications of the branchial arches among various characiforms, Vari (1983:14) hypothesized that the combination of a reduction of the proportional extent of the ossified portion of the first basibranchial in the Prochilodontidae (Vari, 1983, fig. 9), together with a secondary complete loss of the first basibranchial in the Curimatidae (Vari, 1983, figs. 4–6), constituted a synapomorphy for the clade formed by those two families. The more encompassing examination of all members of the Prochilodontidae in this study confirms the generality of the reduction of proportional size of the ossified first basibranchial across that family. Furthermore, the reduction or loss of an ossified first basibranchial is reconfirmed as a synapomorphy for the clade formed by the Prochilodontidae and Curimatidae on the basis of the broader comparative studies across characiforms in this study.

FIRST THROUGH FOURTH CERATOBRANCHIALS.—Characiforms typically have a smooth ventral margin to the anterodorsal face of the first through fourth ceratobranchials. That morphology is found both in proximate outgroups to the Prochilodontidae and within that family in *Ichthyoelephas* and *Semaprochilodus.* Species of *Prochilodus* have instead a series of serrae arrayed along the anterodorsal margins of the first through fourth ceratobranchials with the serrations situated proximate to the ossified bases of the gill filaments, the ossification of which is unique to that genus (Figure 4A,B). The serrae present on these ceratobranchials in *Prochilodus* are comparable in form to those present on the anteroventral margins of the first through third epibranchials, but they are proportionally smaller.

Additionally, the degree of development of the serrae differs between the ceratobranchials, with the processes on the first ceratobranchial typically being smaller than those on the second through fourth ceratobranchials. Ontogenetically the serrations on these ceratobranchials vary from being absent in very small individuals through being limited to the lateral portions of a particular ceratobranchial in small specimens, to progressively extending along a greater proportion of the anteroventral margins of the first through fourth ceratobranchials in cleared and stained specimens of increasing body size. When present, these serrae vary in form and often have their distal portions expanded to varying degrees along the primary axis of the ceratobranchials, even in small specimens. Nonetheless, only in the largest examined cleared and counterstained *Prochilodus* specimen (*P. britskii,* MZUSP 38856, 195.5 mm SL) do the distal portions of adjoining serrations coalesce, at least in part, to form a series of porthole-like openings along the ventral margins of the anterior surface of the first through fourth ceratobranchials (Figure 4B). Larger specimens of *Prochilodus* species that achieve yet larger body sizes, would presumably have the porthole-like openings arrayed along most, or all, of the anterodorsal margins of these ceratobranchials. Such a distal coalescence of adjoining serrae later in ontogeny contrasts with the

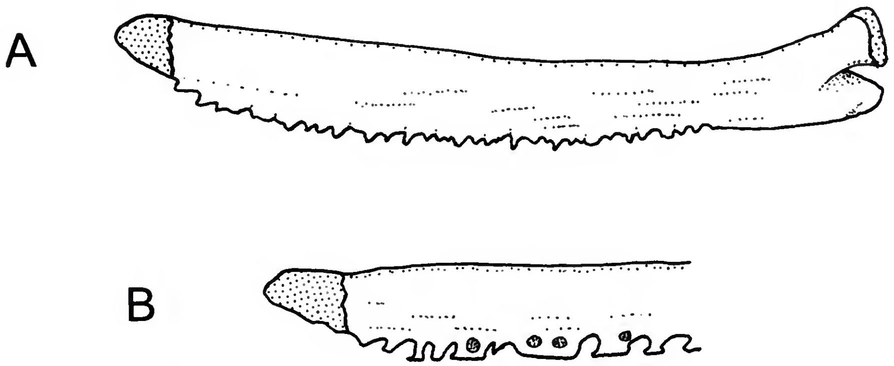


FIGURE 4.—Anterior views of right second ceratobranchial: A, *Prochilodus nigricans*, USNM 32682, showing serrations along ventral margin of anterior surface; B, lateral portion of right second ceratobranchial in *Prochilodus britskii*, MZUSP 38856, showing serrations and porthole-like openings along ventral margin of anterior surface. Dorsal at top and medial at right, with drawings not to scale. (Dense patterned stippling represents cartilage.)

condition of the serrae of the first through third epibranchials of *Prochilodus* species in which distal fusion commences at smaller body sizes. Because of their unique occurrence in *Prochilodus* species among examined characiforms, such serrations and porthole-like openings on the first through fourth ceratobranchials are hypothesized to be a synapomorphy for the species of that genus.

CHARACTER 13. Form of anteroventral margin of the first through fourth ceratobranchials. State 0: Mostly smooth; State 1: With distinct serrae even in smaller specimens and with serrae and porthole-like openings in larger individuals.

FOURTH CERATOBRANCHIAL.—In his analysis of the branchial arches, Vari (1983:13, fig. 7) proposed that the anteromedially directed process on the ventral surface of the fourth epibranchial in the Prochilodontidae and Curimatidae was a synapomorphy for those two families in light of its unique nature among examined characiforms. Previous studies (e.g., Vari, 1989a) found the process to be present in all examined species of the Curimatidae, and the examination of all species of the Prochilodontidae reveals that the process on the ventral surface of the fourth epibranchial is universally present across that family. The possession of that structure is consequently considered to be a synapomorphy for the Prochilodontidae plus Curimatidae.

FIFTH CERATOBRANCHIAL.—Vari (1983:13) hypothesized that the absence of dentition on the dorsal surface of the fifth ceratobranchial was a synapomorphy for the clade that consists of the Prochilodontidae plus Curimatidae. Examination of individuals of smaller sizes than were available in that study (*Prochilodus mariae*, USNM 256959, 18.5 mm SL; *P. nigricans*, LIRP 1312, 12.8–13.6 mm BL), supplemented by literature information (Rossi, 1993:163, fig. 3), demonstrates that the proportionally large dentition on the fifth ceratobranchial present in larvae of the Prochilodontidae undergoes a progressive ontogenetic reduction and eventual loss. At least in *P. lineatus*, the loss of this dentition is correlated with the shift from the zooplanktivorous diet of larvae in the family (Rossi, 1993:164) to the detritivorous and periphyton gathering diet of adult prochilodontids. Such a loss of this dentition is considered to be derived for the clade that consists of the Prochilodontidae plus Curimatidae, given the continued presence of fifth ceratobranchial dentition throughout ontogeny both in proximate outgroups to that clade (Anostomidae, Chilodontidae) and in other groups in the Characiformes. These results are congruent with the hypothesis put forward by Vari (1983) under which the lack of dentition on the dorsal surface of the fifth ceratobranchial was hypothesized to be a synapomorphy for the Prochilodontidae plus Curimatidae.

HYOID APPARATUS

Basihyal

Vari (1983:24, fig. 22b) proposed the pronounced transverse expansion of the anterior portion of the basihyal as a synapomorphy for the species of the Prochilodontidae in light of the unique nature of that modification among characiforms. An examination of samples of all nominal prochilodontid species in this study has confirmed the universal occurrence of a somewhat to distinctly T-shaped basihyal in dorsal view across the family. Further information on this character can be found in Vari (1983:24).

CHARACTER 14. Basihyal form. State 0: Narrow or only moderately widened anteriorly; State 1: Distinctly widened anteriorly.

Dorsal Hypohyal

The dorsal hypohyal of *Prochilodus* and *Semaprochilodus* is characterized by a distinct notch posteriorly (Figure 5A). The sections of the dorsal hypohyal situated on each side of the notch in conjunction with the anterior arms of the anteriorly subdivided anterior ceratohyal encircle a distinct foramen on the dorsolateral surface of the hyoid arch. A comparable aperture also is present in proximate outgroups to the Prochilodontidae and in many outgroup characiforms, and the presence of that opening is hypothesized to be plesiomorphic for the Prochilodontidae. Species of *Ichthyoelephas* have the notch in the posterior portion of the dorsal hypohyal greatly reduced or absent (Figure 5B), a condition considered to be derived within the Prochilodontidae.

CHARACTER 15. Notch on posterior portion of dorsal hypohyal. State 0: Well developed; State 1: Greatly reduced.

In his discussion of the hyoid arch in *Ichthyoelephas,* Roberts (1973:219) indicated that the dorsal and ventral hypophyals were "fused or partially fused." No such fusion of these elements is apparent in the cleared and stained specimens of *Ichthyoelephas* examined in this study.

Anterior Ceratohyal

The anterior ceratohyal is anteriorly bifurcate in the species of *Prochilodus* and *Semaprochilodus,* with the two arms of the bone partially encircling the distinct foramen on the dorsolateral surface of the hyoid arch as noted previously under the discussion of the dorsal hypohyal (Figure 5A). This bifurcation of the anterior ceratohyal, which also is present in the Curimatidae and many outgroup characiforms, is absent in *Ichthyoelephas* (Figure 5B), a derived condition.

CHARACTER 16. Bifurcation on anterior portion of anterior ceratohyal. State 0: Present; State 1: Absent.

Interhyal

Vari (1983:24) hypothesized that the ventrally notched interhyal and the presence of a sesamoid ossification within the ligament that joins the interhyal to the posterior ceratohyal were derived features for the species of the Prochilodontidae, and he treated those jointly as a synapomorphy for the species of the family. Examination of material of all prochilodontid species in this study confirms the presence of these modifications across the family, and outgroup comparisons demonstrate the unique nature of this attribute among examined characiforms. The two attributes (a ventrally notched interhyal and the presence of a sesamoid ossification within the ligament) are together considered a single synapomorphy for consistency with the scheme proposed by Vari (1983:24). Further information on these modifications can be found in that publication.

CHARACTER 17. Form of ventral portion of interhyal and ligament that joins interhyal to posterior ceratohyal. State 0: Ventral portion of interhyal not notched, and ligament between interhyal and posterior ceratohyal without included sesamoid cartilage; State 1: Ventral portion of interhyal notched, and ligament between interhyal and posterior ceratohyal with included sesamoid cartilage.

Branchiostegal Rays

In his analysis, Vari (1983:25) considered the transverse widening of the branchiostegal rays to be a synapomorphy for the species of the Prochilodontidae. The more encompassing intrafamilial examination of branchiostegal rays among the species of the Prochilodontidae confirms the universality of the feature in the family. Further information on this character can be found in Vari (1983).

CHARACTER 18. Form of branchiostegal rays. State 0: Rays narrow or moderately wide; State 1: Rays transversely broad.

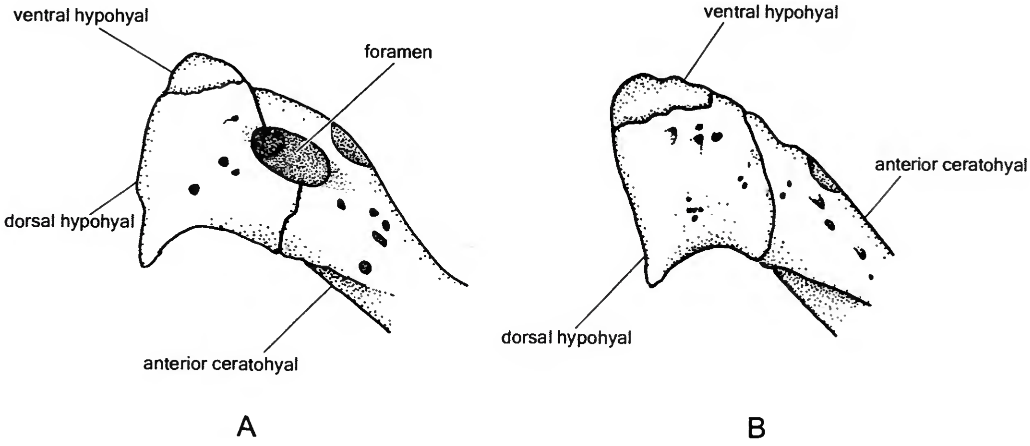


FIGURE 5.—Anterior portion of hyoid arch: A, *Prochilodus nigricans,* USNM 231438; B, *Ichthyoelephas humeralis,* USNM 231437. Dorsal view, anterior at top and medial at left, with drawings not to scale.

Urohyal

The transverse widening of the ventral wings of the urohyal was hypothesized by Vari (1983:25) to be a synapomorphy for the members of the Prochilodontidae. He based this hypothesis upon an examination of a subset of the species in the family. The broader survey within the family in this study found that feature to be universal across the Prochilodontidae. Further information on this synapomorphy can be found in Vari (1983).

CHARACTER 19. Degree of transverse development of ventral wings of urohyal. State 0: Slightly to moderately developed; State 1: Highly developed.

ORAL DENTITION

The form of the oral dentition characteristic of all members of the Prochilodontidae, except during the larval stage, is unique within the Characiformes, both in terms of its unusual form of the association of the teeth with the underlying jaw bones and equally so in terms of the form, arrangement, and total number of functional and replacement teeth. The derived features of the prochilodontid dentition are discussed below by functional units.

Maxillary Dentition

A single row of teeth implanted on the maxilla is typical for characiforms, including the more generalized components of the family Distichodontidae (e.g., *Xenocharax,* see Daget, 1960:39) in the basal clade within the Characiformes. Such a maxillary tooth arrangement also occurs in the families Crenuchidae and Parodontidae, which are similarly hypothesized to be near the base of the intraordinal phylogeny of the Characiformes (Buckup, 1998, fig. 6). Implanted dentition on the maxilla also is present in a variety of taxa across the breadth of the Characiformes, and the possession of such maxillary dentition is consequently considered to be plesiomorphic for characiforms. Looking to proximate outgroups to the Prochilodontidae, we find, however, that maxillary teeth are absent throughout ontogeny in the Curimatidae, the Recent species of which, although edentulous as adults, do have premaxillary and dentary teeth as postlarvae and small juveniles (Vari, 1989a:41; Godoy, 1975:589, 596, 601; see, however, comments below under "Premaxillary and Dentary Dentition" concerning the fossil *Plesiocurimata alvarengai*). Members of the Anostomidae and Chilodontidae, the second outgroup to the Prochilodontidae, also have edentulous maxillae. In the absence of information on the ontogeny of the oral dentition in the Prochilodontidae, Vari (1983:8) noted that it was impossible to determine the homology, or lack thereof, between the oral disk dentition proximate, but not attached, to the maxilla in juvenile and adult prochilodontids and the implanted maxillary dentition that is present in most other groups in the Characiformes. In the absence of that data, Vari (1983) considered it premature to hypothesize that the lack of dentition on the maxilla throughout ontogeny was synapomorphic for the clade that consists of the Prochilodontidae, Curimatidae, Anostomidae, and Chilodontidae. Evidence now permits the resolution of this question.

Ontogenetic information on tooth development in *Prochilodus lineatus* (Rossi, 1993:162) indicates that teeth directly associated with, and attached to, the maxilla are absent throughout ontogeny in that species. Although no cleared and stained, specimens of a prochilodontid of a size comparable to the smallest individuals of *P. lineatus* (7.8 mm BL) examined by Rossi (1993) were available for study in this project, the smallest examined cleared and stained specimen of other members of the family (*P. nigricans,* LIRP 1312, 12.8–13.6 mm BL; and *P. mariae,* USNM 256959, 18.5 mm SL) have the upper-jaw dentition limited to the region proximate to the margin of the premaxilla. The maxilla in these samples is, in turn, edentulous, a finding congruent with the observations of Rossi (1993) for *P. lineatus* specimens of 7.8–14.8 BL. The data, albeit limited to only three species of *Prochilodus,* nonetheless consistently indicate that teeth attached to the posterior portions of the fleshy upper lip in the region proximate to the maxilla in all but larval specimens of the Prochilodontidae do not develop ontogenetically from the dentition originally associated with the maxilla. Rather, the dentition proximate to the maxilla in all but larval prochilodontids originates later in ontogeny from the tooth series that is developmentally originally associated with the premaxilla (Rossi, 1993, fig. 1). Thus, the teeth proximate to, but not attached to, the maxilla in prochilodontids are considered to be non-homologous with the implanted maxillary dentition of other characiforms.

In so far as the possession of implanted maxillary dentition is plesiomorphic within the Characiformes, we hypothesize that the edentulous maxilla present throughout ontogeny in the Prochilodontidae, Curimatidae, Anostomidae, and Chilodontidae is a derived feature. This hypothesized synapomorphy for that four-family clade supplements the four synapomorphies for that clade proposed by Vari (1983:47).

Premaxillary and Dentary Dentition

Postlarval *Prochilodus lineatus* (7.8 mm SL) have five conical teeth in a single series attached to each of the dentaries and premaxillae (Rossi, 1993:162, fig. 1a). With increasing body size the number of teeth in each jaw progressively increases, and by 12.9 mm SL individuals of *P. lineatus* have the dentary and premaxillary dentition arrayed in two irregular rows on each jaw (Rossi, 1993). Our observations indicate that a similar pattern occurs in examined specimens of *P. nigricans* of 12.8–13.6 mm BL (LIRP 1312). Further development results in an increased number of jaw teeth. These later-developing teeth differ from the dentition present earlier in ontogeny in being movably attached to the increasingly fleshy lips rather than demonstrating the usual characiform condition of an attachment to the proximate portions of the dentaries and premaxillae. Despite the lack of contact between these oral teeth and the underlying jaw bones in prochilodontids, these structures are true teeth that demonstrate all the typical features of oral dentition (crown, collar, root, and pulp cavity) except for the lack of implantation on the dentary and premaxilla (Oliveros and Occhi, 1972:132). The teeth originally implanted on the jaws in larvae are lost ontogenetically, and eventually all oral teeth in prochilodontids are solely movably, albeit firmly, associated with the increasingly fleshy lips, thereby rendering both the premaxilla and dentary edentulous in terms of attached dentition.

Outgroup characiforms, including the basal families Citharinidae and Distichodontidae, most typically have moderate- to large-sized implanted teeth arranged in one, two, or less frequently more than two, regularly to irregularly arranged tooth rows on the premaxillae. The dentary has one, or less frequently two, rows of moderate- to large-sized implanted teeth, with the second tooth row, if present, often limited to the anterior portion of the lower jaw, being sometimes represented by a single symphyseal tooth on each side of the jaw. Focusing on proximate outgroups to the Prochilodontidae, we find that very small juveniles of various species within the Curimatidae (Azevedo et al., 1938, figs.1, 2; Godoy, 1975:589, 596, 601; Vari, 1989a:41), the first sister group to the Prochilodontidae, have a single row of teeth on each jaw. Curimatids, however, undergo an ontogenetic loss of oral dentition such that all but juvenile individuals of Recent species of the Curimatidae are invariably edentulous. A single row of "minute conical teeth, in a single series" on the dentary has been reported for an adult fossil curimatid *Plesiocurimata alvarengai* of the Tremembé Formation (Figueiredo and Costa-Carvalho, 1999:889). Oral dentition is, however, absent in a second fossil curimatid, *Cyphocharax mosei* (Malabarba, 1996:58), found in the same geological formation, and a further analysis of the question of oral dentition in fossil curimatids seems appropriate. At most, a single series of jaw teeth is apparently present in one fossil species within the Curimatidae.

Turning to the secondary outgroup to the Prochilodontidae, the clade formed by the Anostomidae plus Chilodontidae, we find that members of the Anostomidae retain a single row of relatively massive, strongly implanted premaxillary and dentary teeth. Although the proportionally large oral teeth in the Anostomidae is unusual, the arrangement of the dentition in those bones, albeit not the absence of teeth on the maxilla, is comparable to that present in many characiforms. Finally, the Chilodontidae, the sister group to the Anostomidae, typically also has a single row of dentition on the premaxilla and dentary, with dentary teeth, however, uniquely absent within that family in *Caenotropus labyrinthicus* (Vari et al., 1995:5; Vari and Ortega, 1997:75). The oral dentition in the Chilodontidae, however, is movably attached to the fleshy lips in a fashion reminiscent to that in the Prochilodontidae. Nonetheless, the tooth form and particularly the form of the tooth replacement rows in the Chilodontidae differs notably from that in the Prochilodontidae (see below). Notwithstanding those differences, the lack of contact of the premaxillary and dentary dentition with the underlying jaw bones in the Prochilodontidae and Chilodontidae is a derived feature within the Characiformes. The overall available morphological evidence (Vari, 1983:46; 1989:50) indicates that the Prochilodontidae and Chilodontidae are not each others closest relatives, a finding corroborated by molecular evidence (Ortí and Meyer, 1997, fig.11), albeit with different conclusions concerning the relationships of the clade formed by Curimatidae plus Prochilodontidae and that formed by the Anostomidae plus Chilodontidae. The overall evidence, nonetheless, indicates that the loss of implanted teeth on the premaxillae and dentaries in the Prochilodontidae and Chilodontidae has been independently acquired and is thus homoplastic in those two families and that this feature is synapomorphic for the species of the Prochilodontidae.

CHARACTER 20. Mode of attachment of teeth on upper and lower jaws. State 0: Teeth directly implanted on dentary and premaxilla; State 1: Teeth not directly implanted on dentary and premaxilla, but rather movably attached to fleshy lips.

Larval prochilodontids have a single row of teeth in each jaw (see Rossi, 1993, fig. 1a–c), a pattern shared with comparably sized individuals of the Curimatidae, larger specimens of which ontogenetically lose that dentition (Azevedo et al., 1938, figs. 1, 2; Godoy, 1975:589, 596, 601; Vari, 1983:41). A single row of teeth in each jaw also occurs in the Chilodontidae and Anostomidae, which together constitute the second outgroup to the Prochilodontidae. Except when larvae, all prochilodontids have two rows of functional teeth in each jaw (Figure 6). The tooth rows in prochilodontids, more strikingly, diverge significantly medially rather than running approximately in parallel as is typical for other characiforms with multiple rows of teeth in one or both jaws. The outer tooth row consists of closely positioned, relatively small teeth arranged along the rim of the fleshy, protrusible jaws. The inner row of functional teeth on each jaw commences medially at a point somewhat to distinctly posterior of the outer row of teeth and angles anterolaterally as an arched series that terminates posteriorly proximate to the outer tooth row. The arrangement of the contralateral inner tooth rows ranges from a shallow arch to an acute V (Figure 6; Oliveros and Occhi, 1972, fig. 1; Rossi, 1993, fig. 2a).

CHARACTER 21. Arrangement of tooth rows in upper and lower jaws. State 0: Tooth rows, when more than one row of teeth present, run approximately in parallel; State 1: Two tooth rows distinctly separated anteriorly, with inner row in curved series approaching outer row of teeth posterolaterally.

In addition to differing from the other taxa in the Characiformes in the relative positions of the two tooth rows in both the upper and lower jaws, prochilodontids are further distinguished from proximate outgroups by their high numbers of functional teeth. This feature was subsumed into a single synapomorphy along with the increased number of functional and replacement tooth rows by Vari (1983). Further analysis indicates that the number of teeth and the number of tooth rows are more appropriately treated independently in this analysis.

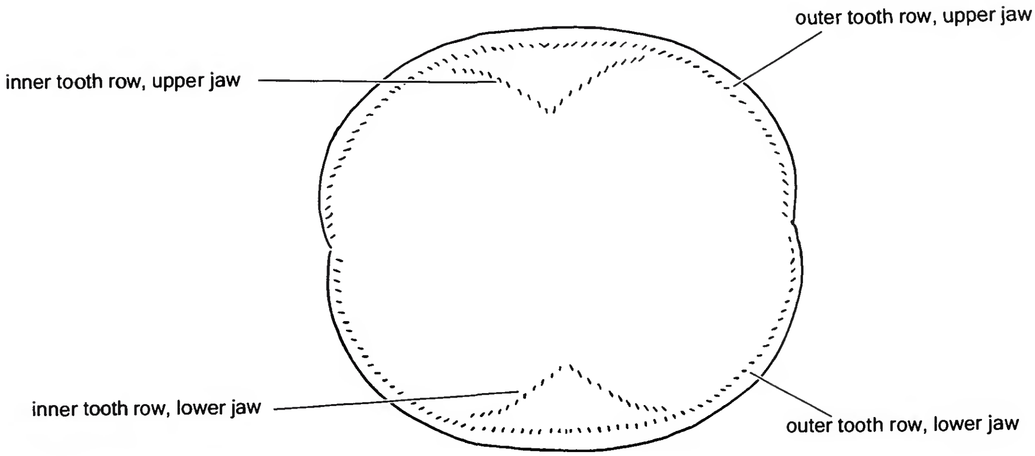


FIGURE 6.—Diagrammatic illustration of the distribution of functional teeth in jaws of *Prochilodus lineatus* (based upon MZUSP 42486). Replacement tooth rows not illustrated.

Prochilodus species in aggregate have 11 to 29 teeth in the inner tooth row series of the upper jaw, *Semaprochilodus* species 8 to 16 teeth in that series, and *Ichthyoelephas* species 27 to 76 teeth in that series, with *I. longirostris* having a notably high value of 50 to 76 teeth, the highest count in any other prochilodontid. Paralleling these ranges in the upper-jaw teeth is variation in the number of teeth in the inner tooth row of the lower jaw. *Prochilodus* and *Semaprochilodus* species have in aggregate 4 to 18 teeth in the inner series of each side of the jaw, whereas *Ichthyoelephas* species have 20 to 70 teeth in that series, with 20 to 39 teeth present in *I. humeralis* and 35 to 70 in *I. longirostris*. Such high numbers of teeth in the inner tooth rows are absent in proximate outgroups, and although comparable numbers of teeth are present in some characiforms (e.g., Ctenoluciidae, Vari, 1995, figs. 24, 25), the outgroup taxa with elevated numbers of teeth are more closely related to groups phylogenetically distant from the Prochilodontidae (see Vari, 1995, concerning Ctenoluciidae). Coding for State 0 is based upon the condition in larvae of the Curimatidae, the first outgroup (oral dentition is absent in Recent adult representatives of that family) and on the condition in the secondary outgroup that consists of the Anostomidae plus Chilodontidae.

CHARACTER 22. Numbers of teeth in inner tooth rows on each side of the upper and lower jaws. State 0: 0 to 7 teeth in each jaw; State 1: 8 to 47 teeth in upper jaw and 4 to 18 in lower jaw; State 2: 50–76 teeth in upper jaw and 20 to 70 in lower jaw.

The only other taxon within the Characiformes that demonstrates an arrangement and form of oral dentition somewhat reminiscent to that in the Prochilodontidae is the Citharinidae, a family that is broadly distributed across sub-Saharan Africa. The Citharinidae shares with the Prochilodontidae both the possession of elongate teeth on the premaxilla and dentary and a single series of functional teeth along the margins of the jaws, but with notable differences in details of this dentition. The series of teeth in the upper and lower jaws of the Citharinidae are separated by a distinct gap posteriorly at the rictus of the mouth. Such a pronounced gap, the plesiomorphic condition for characiforms, contrasts with the nearly continuous ring of teeth around an evertable oral disk that is a characteristic of the Prochilodontidae. Furthermore, the oral dentition in all genera of the Citharinidae lacks the multiple rows of replacement teeth typical of the Prochilodontidae (see discussion below), and the teeth in the Citharinidae are relatively straight and distinctly bifurcate distally (see Daget, 1962a:510; 1962b:91), a morphology very different from the angled and spatulate or falcate teeth present in the Prochilodontidae (see descriptions below). Above and beyond these morphological differences in various details of the oral dentition, the Citharinidae is most closely related to the African family Distichodontidae (Vari, 1979), with that two-family lineage, in turn, basal within the phylogeny of the Characiformes (Buckup, 1998) and, thus, distinctly separate phylogenetically from the Prochilodontidae.

The similarities between the arrangement of the oral dentition in the Prochilodontidae and Citharinidae are most parsimoniously hypothesized to be homoplastic, given that these taxa are not sister groups (Vari, 1979, 1983) and apparently reflect ecological parallelisms associated with the exploitation by these families of similar food items in South American and African freshwaters, respectively. The Citharinidae is one of the three major groups of detritus-feeding fishes in Africa (Bowen, 1984:138), and at least *Citharinus*, the genus that includes most of the species in the Citharinidae, is reported to be a "microphage" that feeds on "vase organique" (=organic debris) (Daget, 1962b:87; Gosse, 1990:265), an energy source comparable to that exploited in the Neotropics by the Prochilodontidae.

Replacement Tooth Rows

One of the most striking aspects of the oral dentition in the Prochilodontidae is the numerous replacement tooth rows present in adults of the family. Starting with a single row of teeth in very small individuals, prochilodontids undergo an ontogenetic increase in the number of rows of replacement teeth in each jaw (Rossi, 1993, fig. 1), with up to 22 series arranged in discrete bands present in large individuals of some species (e.g., *Ichthyoelephas longirostris*). The mode and frequency of tooth replacement within the Prochilodontidae has yet to be investigated, although Oliveros and Occhi (1972:129, table 1) found that there is a progressive increase in the percentage of teeth in the process of replacement with increasing body size. They determined that large individuals (425–475 mm SL) of *Prochilodus lineatus* (the *P. platensis* of those authors) have approximately 20%–25% of the teeth in the jaws in the process of replacement at any one time. The numerous replacement teeth series in members of the family are presumably correlated with this relatively high rate of tooth replacement that may reflect damage to, or loss of, teeth during the scrapping of detritus and aufwucks from hard substrate surfaces during feeding activities. Proximate outgroups to the Prochilodontidae either have a single functional tooth row as larvae that is lost ontogenetically without any replacement teeth (Curimatidae) or have the replacement dentition limited to a single series in each jaw (Anostomidae, Chilodontidae). Although some large individuals of *Distichodus* have a series of replacement teeth (Roberts, 1967, fig. 6), a pattern of numerous replacement tooth rows, such as occurs in the Prochilodontidae, is not approximated elsewhere within the Characiformes, and the condition in the Prochilodontidae is consequently hypothesized to be derived.

Vari (1983:9, 26) subsumed the increased number of functional teeth and the high number of replacement tooth rows into a single synapomorphy for the members of the Prochilodontidae. Further analysis has shown that we are dealing with two different, albeit associated, systems; consequently, they are treated as separate characters herein.

CHARACTER 23. Number of replacement tooth rows. State 0: 1; State 1: 2 to 22.

Tooth Form

Two general patterns of tooth form occur in the Prochilodontidae, both of which are characterized by a distinctive curvature of the teeth towards the bucco-pharyngeal cavity in the closed mouth. *Prochilodus* and *Semaprochilodus* have somewhat elongate, curved, distally expanded teeth (Figure 7A), the exposed surfaces of which overlap to varying degrees sequentially. *Ichthyoelephas* species have particularly elongate teeth with a pronounced curvature of the teeth beyond the condition elsewhere in the family (Figure 7B). As a consequence, the teeth in *Ichthyoelephas* have a falcate form with a pronounced angle between the main axes of the basal and main portions of the tooth. Although the polarity of the two forms of oral dentition in the Prochilodontidae is uncertain, the overall form of the jaw teeth that is typical for members of that family is unknown elsewhere among characiforms and is considered to be derived.

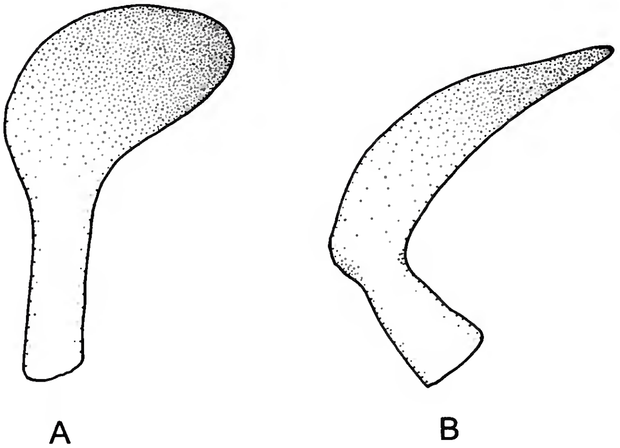


FIGURE 7.—Anterolateral view of functional oral teeth: A, *Prochilodus mariae*, USNM 270243; B, *Ichthyoelephas humeralis*, USNM 290374. Teeth were taken from upper jaw, right side.

CHARACTER 24. Form of jaw teeth. State 0: Not as in state 1; State 1: Teeth elongate, curved or falcate, with distinct orientation towards the bucco-pharyngeal cavity.

LIPS

The possession of fleshy lips that are evertable into an oral disk encircled by a series of numerous small teeth (see Figure 6 for tooth arrangement) is the externally most distinctive feature of the members of the Prochilodontidae. Such pronounced lip eversion is made possible by a series of modifications of various osteological and soft internal anatomical systems that are discussed in other sections. Independent of those associated features, various aspects of the lips are themselves distinctive for the Prochilodontidae within the Characiformes.

All but larval prochilodontids have the lips distinctly to significantly expanded into fleshy pads (see illustrations of species herein) that are broadly joined together at the posterior corner of the mouth and form a continuous oral disk. No such pronounced expansion of the lips and extensive posterior union of the upper and lower lips occurs in other characiforms, and these features are in combination considered to be derived. In addition, the posterior portion of the lower lip of prochilodontids differs from the condition typical for characiforms in the absence of a direct attachment of the margins of the lip to the lateral margins of the underlying bones. Rather, prochilodontids have a deep indentation between the lips and the lower jaw posteriorly, with the attachment of the lower lip to the underlying jaw situated distinctly medial of the lateral margin of the lower jaw. This indentation and the consequent mobility of the fleshy lips relative to that portion of the lower jaw is correlated with the pronounced evertability of the jaws.

CHARACTER 25. Form of lips. State 0: Lips effectively absent to slightly fleshy, not broadly in contact posteriorly, and with lower lip directly attached to lateral margin of lower jaw; State 1: Lips enlarged and developed into fleshy pads broadly in contact posteriorly to form oral disk, with attachment of lower lip distinctly medial of lateral margin of lower jaw.

The lower jaw in the Prochilodontidae also is characterized by a laterally positioned, ledge-shaped process formed of stiff connective tissue that extends along the external surface of the lower jaw immediately below the ventral portion of the lower lip. This process apparently provides support for the ventral surface of the lower lip when the mouth is closed, and it contributes to the smooth profile along that portion of the head, presumably thereby contributing to a laminar water flow over the ventral surface of the head. Such a structure has not been found in other examined characiforms, and its possession is consequently hypothesized to be derived.

CHARACTER 26. Laterally positioned, ledge-shaped process formed by connective tissue under margin of lower lip. State 0: Absent; State 1: Present.

The range of development of the lips within the Prochilodontidae is rather variable but is always distinctly enlarged relative to the condition in other characiforms (e.g., the sister group, Curimatidae; see *Cyphocharax leucostictus,* Vari, 1992, figs. 10, 11). The degree of development of the lip is most pronounced in the species of *Ichthyoelephas* (Figures 29, 31) that have a massively developed upper lip that distinctly overhangs the anterior limit of the lower jaw. In light of the absence of such a pronounced development of the upper lip elsewhere among characiforms, the more expansive upper lip in *Ichthyoelephas* is considered to be derived.

CHARACTER 27. Relative size of fleshy lips. State 0: Upper and lower jaws about equally developed; State 1: Upper lip very large and distinctly overlapping lower lip.

UPPER JAW

Above and beyond the series of modifications of the maxilla and premaxilla discussed in the following sections, one of the striking aspects of the upper jaw in prochilodontids is the position of the upper-jaw bones relative to the adjoining structures of the anterolateral surface of the head. The Curimatidae, Anostomidae, and Chilodontidae, the proximate outgroups to the Prochilodontidae, have the distal portion of the maxilla mostly, if not completely, visible from a lateral view when the mouth is closed. Such a lateral exposure of the maxilla also occurs in more distantly related groups of characiforms (e.g., *Brycon meeki,* Weitzman, 1962, fig. 8; *Hoplias* and *Salminus,* Roberts, 1969, figs. 3, 4), including the families Citharinidae (e.g., *Citharidium,* Daget, 1962a, fig. 10) and Distichodontidae (e.g., *Xenocharax,* Daget, 1960, fig. 7; *Neolebias,* Daget, 1965:7) that together form the basal lineage within the Characiformes. Usually among characiforms the posterior portion of the maxilla lies approximately in the same parasagittal plane as the outer margin of the ventral wing of the lateral ethmoid.

Correlated with the various pronounced modifications of the premaxilla and maxilla in the Prochilodontidae is the shift medially of the entire upper-jaw complex. As a consequence, the maxilla in prochilodontids is positioned distinctly more medially relative to the adjoining ossifications of the lateral portion of the head than is the condition typical for characiforms. This medial shift of the upper jaw is best reflected in the complete, or near complete, overlap in the closed mouth of the lateral portion of the maxilla by the first infraorbital across the Prochilodontidae. A second consequence of this repositioning of the upper jaw in the Prochilodontidae is the proximity of the posterior portion of the maxilla to the anteromedial surface of the ventral wing of the lateral ethmoid and to the ventral surface of the connective tissue sheet that forms the floor of the nasal capsule. Such a location contrasts with the location of the posterior portion of the maxilla near the lateral margin of the lateral ethmoid in other characiforms. Because of its unique nature within the Characiformes, including basal groups in the order (Citharinidae, Distichodontidae), this medial shift of the position of the posterior portion of the upper jaw in all species of the Prochilodontidae is hypothesized to be derived.

CHARACTER 28. Position of the maxilla. State 0: Lateral surface of maxilla approximately in same parasagittal plane as first infraorbital with little overlap of maxilla by first infraorbital and with the posterior portion of the maxilla situated proximate to the lateral margin of the anteroventral wing of the lateral ethmoid; State 1: Lateral surface of the maxilla mostly overlapped by first infraorbital in closed mouth with posterior portion of maxilla situated proximate to anteromedial surface of ventral wing of lateral ethmoid.

Another unusual aspect of the prochilodontid upper jaw is its degree of mobility relative to the ventromedially enlarged mesethmoid that is characteristic of the family. In the proximate outgroups to the Prochilodontidae, the families Curimatidae, Chilodontidae, and Anostomidae, the upper jaw is only moderately mobile with respect to the neurocranium. Upper-jaw motion in these outgroups to the Prochilodontidae is a function of the hinging of the premaxillae on the anterior portion of the mesethmoid, with the degree of motion limited by the tight connective tissue linkage between those ossifications. The form of mobility in those outgroup families is widespread across the Characiformes, including basal lineages; therefore, it is considered to be the primitive condition within the order. The prochilodontid upper jaw, in contrast, lacks a very close connective tissue linkage between the mesethmoid and the premaxilla. Rather, the looser connective tissue bands that join these ossifications permit an increased degree of mobility between the upper jaw and the neurocranium as reflected in the moderate anterior-posterior horizontal motion of the anterome-

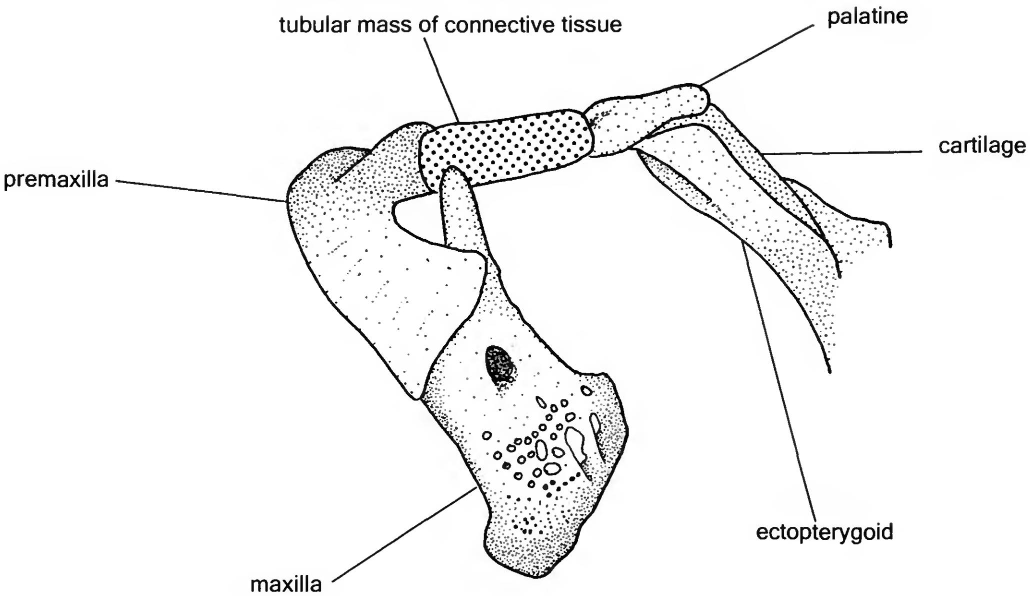


FIGURE 8.—Upper jaw and anterior portions of suspensorium in *Prochilodus rubrotaeniatus*, USNM 225419, left side, lateral view, showing form and position of approximately tubular mass of connective tissue between palatine, premaxilla, and maxilla. Jaw bones rotated anteroventrally from position in closed mouth and with functional and replacement rows of oral dentition not illustrated.

dial surface of the premaxilla along the horizontally elongate lateral articular surface of the ventromedial process of the mesethmoid in all prochilodontids. This is hypothesized to be a derived condition.

CHARACTER 29. Form of junction between premaxilla and mesethmoid and degree of mobility between those elements. State 0: Premaxilla relatively tightly joined to the mesethmoid, with premaxilla hinged on mesethmoid; State 1: Premaxilla somewhat loosely joined to mesethmoid, with resultant degree of anterior-posterior motion of premaxilla along anterolateral surface of mesethmoid.

Soft Tissues

The lack of a tight connection between the premaxilla and the lateral margin of the mesethmoid in the Prochilodontidae is paralleled by changes in the connections between the upper-jaw bones and the palatine. Looking to proximate outgroups to the Prochilodontidae, we find that the Curimatidae has an irregularly shaped cartilage situated between the anterodorsal portion of the palatine, the anterodorsal portion of the maxilla, and the posterodorsal portion of the premaxilla (cartilage illustrated but not labeled in Vari, 1983, fig. 25). A similar cartilage is present in examined species of the Anostomidae. Members of the Prochilodontidae lack the irregular cartilage situated in the area of the junction of the maxilla, premaxilla, and palatine; instead, they have a discrete, approximately tubular mass of connective tissue in that position (Figure 8). This structure extends anteriorly from both the medial surface of the anterodorsal portion of the palatine and the dorsolateral surface of the cartilage mass that is enveloped marginally to varying degrees by the ectopterygoid and palatine. From that location, the tubular connective tissue body continues anteriorly to both the anteromedial surface of the ascending process of the maxilla and to the posterodorsal process situated on the posteriorly curved medial portion of the premaxilla. The composition of this tubular body in the Prochilodontidae remains undetermined. Although this structure is reminiscent of cartilage in being flexibly rigid and in some specimens being somewhat transparent, it fails to stain with Alcian Blue, which is contrary to the cartilage body found in this region in some proximate outgroups to the family that includes the Curimatidae. Regardless of its composition, outgroup comparisons failed to reveal any comparable structure among other characiforms, and its possession is considered to be a synapomorphy for the Prochilodontidae.

The connection between the anterodorsal portion of the suspensorium and the upper jaw in the Chilodontidae, a member of the secondary outgroup to the Prochilodontidae, also differs from the condition typical within the Characiformes. Chilodontids have a notably restructured upper jaw with an enlarged maxilla that excludes the palatine from contact, or near contact, with the premaxilla that is nearly universal among other characiforms. Furthermore, chilodontids lack the discrete cartilage mass that is present in the area of proximity of those ossifications in all examined members of their sister group, the Anostomidae. Although the presence of a non-Alcian Blue

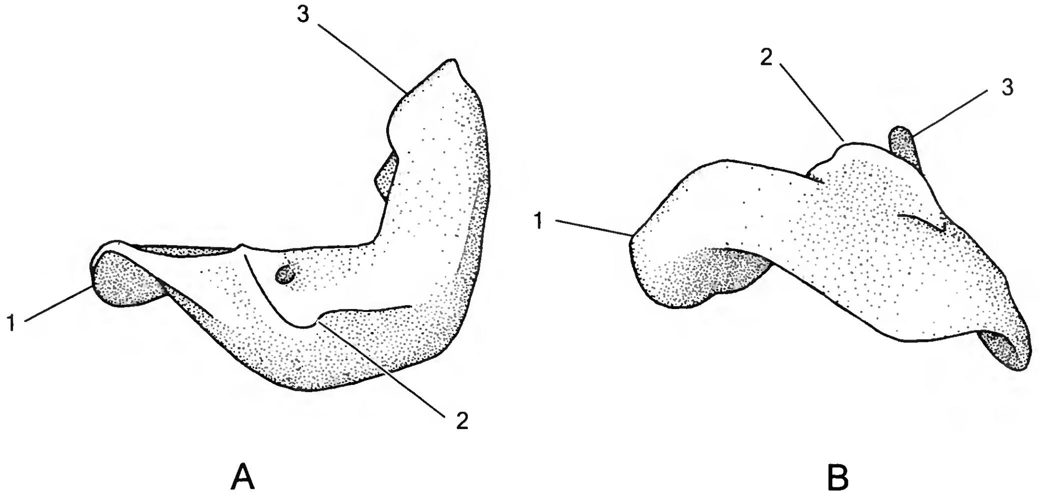


FIGURE 9.—*Prochilodus rubrotaeniatus*, USNM 225419, premaxilla: A, dorsal view, medial at left, anterior at bottom; B, anteromedial view, medial to left, dorsal at top. Numbers indicate comparable landmarks.

staining connective tissue mass instead of a discrete Alcian Blue staining cartilage in the area between the palatine and the maxilla in the Chilodontidae is reminiscent in these details to the lack of the cartilage in the Prochilodontidae, the connective tissue system between the upper jaw and the suspensorium in the Chilodontidae differs from that in the Prochilodontidae both in its diffuse nature and in its lack of the distinct tubular form of the connective tissue mass situated in that region in the Prochilodontidae. These anatomical differences and the available phylogenetic evidence that indicates that the Prochilodontidae and Chilodontidae are not sister taxa (Vari, 1983, 1989a; Ortí and Meyer, 1997) leads us to conclude that the connective tissue complexes present between the upper jaw and the palatine in those two families are non-homologous.

CHARACTER 30. Non-ossified tissues at junction of premaxilla, maxilla, and palatine. State 0: Not as in State 1; State 1: Discrete, approximately tubular mass of connective tissue present in region of junction of premaxilla, maxilla, and palatine.

Bones

The pronounced restructurings of the lips and the series of modifications of the functional and replacement tooth rows in the upper jaw in the Prochilodontidae are reflected in significant alterations of the underlying premaxilla and maxilla relative to the conditions of those ossifications found in all other characiforms. We discuss each of the modifications separately, with orientations presented in terms of the positions of these bones in the closed mouth during which the upper jaw assumes in a nearly horizontal orientation.

Premaxilla

In the Curimatidae, the sister group to the Prochilodontidae, the premaxillae are slightly curved as they extend laterally, with the contralateral ossifications in contact anteromedial to the mesethmoid. Each premaxilla bears a distinct articular facet along its anterodorsal corner that contacts the proximate anterolateral surface of the mesethmoid. Juvenile prochilodontids of less than approximately 12–14 mm SL have near contact of the medial portions of the contralateral premaxilla anterior to the mesethmoid (e.g., *Prochilodus lineatus*, see Rossi, 1993, fig. 1; *P. nigricans*, pers. observ.), a condition that approximates that present in adults of the Curimatidae and many other clades within the Characiformes. The medial portions of the premaxilla in such small prochilodontid specimens are, in addition, smoothly continuous with the portions of the ossification situated posterior of the articular facet, another condition that approximates those found in outgroup characiforms.

In the course of their ontogeny, all species of the Prochilodontidae dramatically modify the just-described form of the premaxilla; this restructuring markedly alters not only the overall morphology of the bone (Figures 8–11) but also its association with adjoining ossifications. In all but the smallest examined specimens of the Prochilodontidae, the portion of the premaxilla medial to the facet for articulation of that ossification with the mesethmoid is remodeled into a complex, twisted process that first extends medially, then ventrally, and finally anteriorly (Figure 9). This revamping shifts the area of contact between the contralateral premaxillae to a position ventral of the anterior articular portion of the mesethmoid—a location distinctly posteroventral of the usual area of contact of those bones among characiforms. The Prochilodontidae also has the portion of the premaxilla situated lateral of the articular facet notably modified relative to the morphology of that region in outgroups, being developed in all but very small juveniles into a broad, posteriorly curving surface that is distinctly laterally

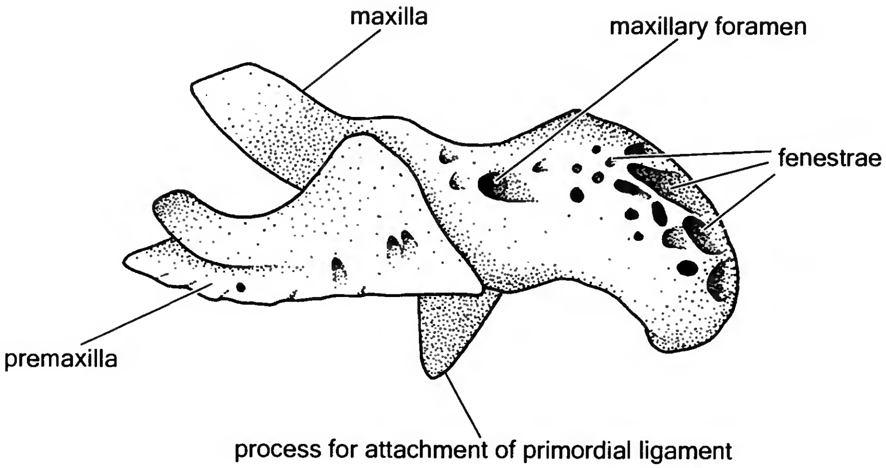


FIGURE 10.—*Prochilodus vimboides,* USNM 345752, bones of upper jaw, lateral view, anterior at left, dorsal at top. Jaw bones positioned as in closed mouth.

convex in cross section. These restructurings of the premaxilla are unique to the members of the Prochilodontidae within the Characiformes and are hypothesized to be synapomorphies for the species of the family.

CHARACTER 31. Overall form of the premaxilla. State 0: Premaxilla gently curved overall and relatively flat posteriorly, with medial portions of contralateral premaxillae in near contact anterior to the mesethmoid; State 1: Premaxilla with anteromedial portion restructured into twisting structure and posterior region distinctly laterally convex in cross section, with medial portions of contralateral premaxillae shifted to ventral of anterior articular portion of mesethmoid.

Further modifications of the premaxilla are phylogenetically informative for components of the Prochilodontidae. *Ichthyoelephas* species have premaxillae that are proportionally much more extensive vertically than those present in either *Prochilodus* and *Semaprochilodus* or proximate outgroups to the Prochilodontidae (Figure 11). *Ichthyoelephas* species also have a distinct articular surface on the posterodorsal portion of the premaxilla that contacts a corresponding articular surface of the maxilla. The vertical expansion of the premaxilla and its possession of the posterodorsal articular facet are both features unique to *Ichthyoelephas* among examined characiforms.

CHARACTER 32. Vertical extent of posterior portion of premaxilla and form of contact between premaxilla and maxilla. State 0: Posterior portion of premaxilla moderately high and without distinct articular surface in area of contact with maxilla; State 1: Posterior portion of premaxilla vertically expanded and with distinct posterodorsal articular surface in area of contact with maxilla.

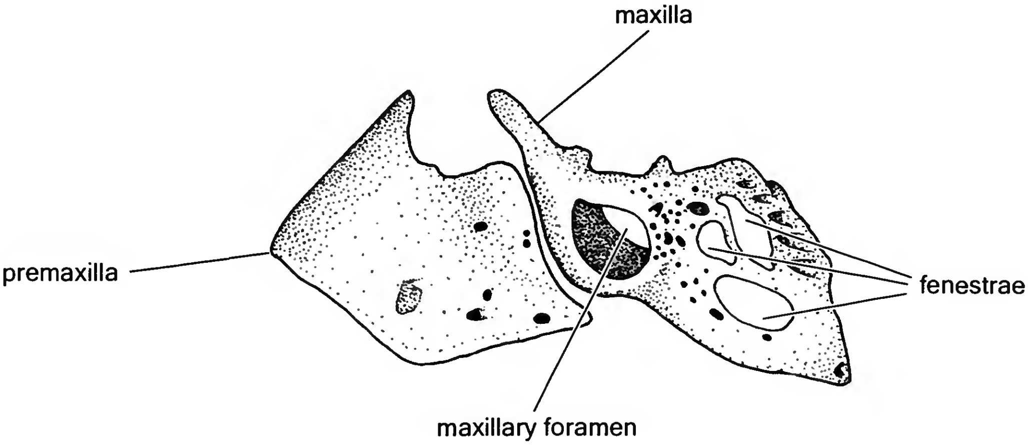


FIGURE 11.—*Ichthyoelephas humeralis,* USNM 231437, bones of upper jaw, lateral view, anterior at left, dorsal at top. Jaw bones positioned as in closed mouth.

In *Semaprochilodus* species, the anteroventral portion of the premaxilla is rotated anteriorly as a distinct process somewhat reminiscent in form to a hat brim. Associated with these modifications to the outer surface of the premaxilla is the development of a distinct ridge along the inner surface of that ossification in all *Semaprochilodus* species. These restructurings of the premaxilla are hypothesized to be a synapomorphy for the members of *Semaprochilodus,* given their absence in other prochilodontid genera and examined outgroups.

CHARACTER 33. Form of anteroventral margin and medial surface of premaxilla. State 0: Anteroventral margin smooth and without distinct process on inner surface; State 1: Anteroventral margin rotated anteriorly to form process in form somewhat resembling a hat brim and with distinct ridge on inner surface of bone.

Correlated with the pronounced restructuring of the premaxilla in the Prochilodontidae is the development of a soft tissue system that is unique to the family within examined characiform taxa. Outgroups to the Prochilodontidae lack well-developed, ligamentous bands that extend between the opposite parts of the premaxilla. Prochilodontids, in contrast, have a well-developed ligament that extends between the posteromedial surface of the anteroventral process of the bone and the medial surface of the posterior portion of the ossification. This ligament, in conjunction with the curvature of the premaxilla, results in a bow-like complex unique to the Prochilodontidae within the Characiformes. The possession of the ligament between the two opposite portions of the premaxilla is consequently considered to be a synapomorphy for the species of the Prochilodontidae.

CHARACTER 34. Ligament that extends between posteromedial surface of anteroventral process of premaxilla and posterior portion of premaxilla. State 0: Absent; State 1: Present.

Maxilla

The maxilla of prochilodontids is highly restructured relative to the condition of the ossification in all other characiforms; these modifications were previously discussed, in part, by Vari (1983) and were based upon an examination of a subset of the species in the family. The most readily apparent of these modifications, found in all prochilodontids in this study, is the well-developed, longitudinal and vertical curvature of the posterior region of the maxilla that results in a distinct, laterally convex, helmet-shaped posterior portion of the maxilla when examined from a lateral view (Figures 8, 10, 11). Outgroup characiforms have a variably transversely flattened to slightly convex maxilla, but in none of these taxa does that bone demonstrate the pronounced lateral convexity universal among prochilodontids. That remodeling of the maxilla is consequently considered to be derived and synapomorphic for the members of the Prochilodontidae.

CHARACTER 35. Overall form of maxilla. State 0: Maxilla relatively flat to slightly convex; State 1: Maxilla distinctly laterally convex both longitudinally and vertically, with posterior portion consequently helmet-shaped from lateral view.

The portion of the maxilla proximate to the posterior margin of the bone in the Prochilodontidae has dorsal and ventral processes that extend beyond the main body of the ossification (Figure 2). Associated with these processes is a thickening of the posterior region of the maxilla, which in large specimens forms a distinct ridge that extends the length of the posteromedial portion of the maxillae. This thickened posterior portion of the maxilla significantly stiffens the distal portion of that ossification and may compensate structurally for the numerous fenestrae that pierce, and likely reduce the strength of, that region of the bone in all genera of the Prochilodontidae (see discussion below). Such dorsal and ventral expansions of the maxilla and the thickening of the distal margin of that bone are absent in other examined taxa in the Characiformes, and their possession is consequently considered to be a synapomorphy for the Prochilodontidae.

CHARACTER 36. Posterior portion of maxilla. State 0: Not thickened and without dorsal and ventral extensions; State 1: Distinctly thickened and with dorsal and ventral extensions.

Intrafamilial variation exists in the form of the distal margin of the maxilla. In *Ichthyoelephas* species, the posterior portion of the maxilla is restructured into a posteroventrally angled structure with a distinctly posteroventrally pointed profile (Figure 11). Associated with the restructuring of the overall form of the maxilla is the shift anteriorly of the dorsal process that caps the posterior thickened region of the bone relative to the position of that process in *Semaprochilodus* and *Prochilodus*. Neither of these modifications of the maxilla occur in other prochilodontids nor are they present in outgroup characiforms, and both are hypothesized to be derived and synapomorphic for the species of *Ichthyoelephas*.

CHARACTER 37. Overall form of distal portion of maxilla. State 0: Not as in State 1; State 1: Maxilla restructured into posteroventrally angled structure with distinct point and shift anteriorly of dorsal process that caps thickened posterior portion of bone.

Vari (1983:10) noted that the series of foramina concentrated in the distal portion of the maxilla in various prochilodontids was a most unusual feature for characiforms. He proposed, based on the examination of a subset of the species in the family, that the presence of such openings was a synapomorphy for the members of that family. Further analysis in this study has shown that this feature is present in all members of the Prochilodontidae (Figures 8, 10, 11) and is indeed synapomorphic for the species of the family.

CHARACTER 38. Series of foramina through posterior portion of maxilla. State 0: Absent; State 1: Present.

More encompassing examinations during this study have revealed generic-level variation in the relative proportions of the foramina through the posterior portion of the maxilla. In the species of *Prochilodus* (Figures 8, 10), the majority of the openings are relatively small, whereas *Ichthyoelephas* (Figure 11) and

Semaprochilodus have proportionally distinctly larger foramina. The absence of such maxillary foramina in outgroup characiforms makes it impossible to determine the polarity of the relative size of the openings, but the possession of larger openings is optimized as a synapomorphy for *Ichthyoelephas* and *Semaprochilodus* within the most parsimonious overall analysis arrived at in this study (see "Phylogenetic Reconstruction").

CHARACTER 39. Relative size of the foramina through posterior portion of maxilla. State 0: Small; State 1: Large.

In addition to the series of foramina on the distal half of the maxilla, the species of the Prochilodontidae also have a distinct opening on the lateral surface of that ossification. This aperture is situated in the region somewhat posterior of where the rear margin of the premaxilla extends over the maxilla. In the species of *Prochilodus* (Figures 8, 10) and *Semaprochilodus*, this aperture, hereafter termed the maxillary foramen, opens into a canal that extends in an approximately horizontal direction through the main body of the bone to exit further anteriorly on the medial surface of the maxilla. The species of *Ichthyoelephas*, in contrast, have a large maxillary foramen in that portion of the maxilla (Figure 11), albeit with different degrees of development in the two species. In *I. longirostris*, the foramen is moderately developed, although distinctly larger than the opening present in the species of *Prochilodus* and *Semaprochilodus*, whereas *I. humeralis* has a proportionally larger aperture of a size unique to, and apparently autapomorphic for, that species. The enlarged maxillary foramen in *Ichthyoelephas* encompasses the entire region occupied by the canal system in *Prochilodus* and *Semaprochilodus* and, as a result, passes directly through the maxilla rather than angling anteriorly to a horizontally displaced opening on the medial surface of the bone, such as occurs in the two latter genera. The purpose of the maxillary foramen in the Prochilodontidae is undetermined. Although the two forms of the maxillary foramen (a canal in *Prochilodus* and *Semaprochilodus* and an enlarged foramen in *Ichthyoelephas*) differ in size and orientation, such an aperture is absent in examined outgroups. The possession of a maxillary foramen by all members of the Prochilodontidae is, therefore, considered to be synapomorphic for the species of the family.

CHARACTER 40. Foramen through maxilla in region slightly posterior of where rear margin of premaxilla extends over maxilla. State 0: Absent; State 1: Present.

Turning to the anterior portion of the maxilla in prochilodontids, we find several modifications pertinent to questions at different taxonomic levels. Perhaps the most striking of these is the restructuring of the portion of the maxilla that serves as the area for attachment for the primordial ligament (see also below under the discussion of that ligament). In outgroup characiforms, the region of the maxilla onto which the ligament attaches is either unelaborated or has at most a small ridge that presumably serves to increase the attachment area for the ligament. In all members of the Prochilodontidae, in contrast, there is a highly developed, elongate process on the maxilla that extends ventrally distinctly beyond the margin of the anterior portion of the main body of the maxilla (Figure 10). The ventral portion of the process is thickened and rotated somewhat anteriorly and consequently forms an attachment area for the anterior terminus of the primordial ligament. The development of such a process and the consequent shift of the attachment of the primordial ligament away from its usual site of attachment on the main body of the maxilla to the tip of the process may be functionally associated with the highly evertable jaws that are diagnostic of the Prochilodontidae. Such a lever-like process on the maxilla would provide a mechanical advantage during feeding by facilitating the rapid and/or forceful closure of the large, fleshy, protracted jaws that are present in all prochilodontids. No such process of the maxilla is known to occur in any other component of the Characiformes, and the possession of this structure in the Prochilodontidae is hypothesized to be derived.

CHARACTER 41. Attachment area of primordial ligament on maxilla. State 0: On main body of bone; State 1: On distal tip of highly developed process that extends distinctly beyond margin of anterior portion of maxilla.

Several further elaborations of the just-described maxillary process that is common to all members of the Prochilodontidae are phylogenetically informative at intrafamilial levels. In *Ichthyoelephas*, the attachment area of the ligament on the lever-like process of the maxilla is expanded beyond the condition present in *Prochilodus* (Figure 10) and *Semaprochilodus* by way of a posterior extension of the portion of the region of the process onto which the ligament attaches, a further derived condition that is synapomorphic for that genus. Furthermore, the ventral process of the maxilla onto which the primordial ligament attaches distally is approximately triangular in the species of *Prochilodus* and *Semaprochilodus*, with the anterior margin of the process serving as an area of attachment for various bands of connective tissue except the primordial ligament. In *Ichthyoelephas*, the ventral process extends further anteriorly, with a distinct portion of the structure situated anterior to the region where these other bands of connective tissue attach onto the process. In the absence of such a maxillary process in outgroup taxa, the outgroup condition is coded as unknown, and it is impossible to polarize the two conditions in the Prochilodontidae. The more extensive process present in *Ichthyoelephas* is optimized as derived within the overall most parsimonious phylogenetic reconstruction (see "Phylogenetic Reconstruction").

CHARACTER 42. Morphology of area of process on the maxilla onto which primordial ligament attaches. State 0: Not as in State 1; State 1: With posterior extension of main body of process.

The anterodorsal margin of the anterior portion of the triangular process onto which the primordial ligament attaches has a distinct ridge in the species of *Semaprochilodus*. This ridge, situated proximate to the region where the maxilla contacts the premaxilla, is absent in both *Ichthyoelephas* and *Prochilodus*, and the possession of that process is consequently considered to be a synapomorphy for the species of *Semaprochilodus*. Within the latter genus, the ridge is particularly well developed dorsally beyond the condition present in their congeners in *S. insignis* and *S. kneri*, a further derived condition.

CHARACTER 43. Ridge on anterodorsal margin of triangular process onto which primordial ligament attaches. State 0: Not present; State 1: Present and only moderately developed dorsally; State 2: Present and well developed dorsally.

The anterodorsal portion of the maxilla movably contacts the adjoining region of the premaxilla without a distinct articular facet in the species of *Prochilodus*, or such a facet, if present, is only apparent, but not particularly distinct, in the larger of the examined cleared and stained specimens of various species of the genus. Cleared and stained specimens of all sizes of *Ichthyoelephas* and *Semaprochilodus* instead have a distinct articular facet on the anterodorsal portion of the maxilla delimited by a dorsally expanded ridge that matches the contours of the corresponding portion of the premaxilla. This facet is particularly well developed in larger examined cleared and stained individuals of both genera. The condition of the maxilla in these genera is hypothesized to be derived, given the lack of such modifications in proximate outgroups to the Prochilodontidae. In *Ichthyoelephas*, the articular surface of the maxilla is particularly well developed relative to the condition in both *Prochilodus* and *Semaprochilodus*, a synapomorphy for the species of that genus.

CHARACTER 44. Facet on anterodorsal portion of maxilla in area of contact with premaxilla. State 0: Absent or only present as indistinct structure in large specimens; State 1: Present in all but small specimens; State 2: Present and well developed in both small and large specimens.

The dorsal margin of the maxilla is relatively smooth in both *Prochilodus* and proximate outgroups to the Prochilodontidae. In *Ichthyoelephas* and *Semaprochilodus*, that portion of the bone has a varyingly developed process that serves as an area of attachment for various connective tissue bands. In light of its unique nature, this elaboration of the dorsal margin of the maxilla is hypothesized to be derived and, thus, synapomorphic for *Ichthyoelephas* and *Semaprochilodus*.

CHARACTER 45. Form of dorsal margin of maxilla. State 0: Relatively smooth and without distinct process; State 1: With distinct process that serves as attachment area for connective tissue bands.

A final modification of note in the maxilla of the Prochilodontidae involves the ascending process of that bone. In outgroups to the Prochilodontidae and in species of *Prochilodus* and *Ichthyoelephas*, the ascending process is relatively straight, a condition considered to be primitive based upon outgroup comparisons. In the species of *Semaprochilodus*, the dorsal portion of the ascending process of the maxilla is instead bent somewhat laterally, a derived modification.

CHARACTER 46. Form of ascending process of maxilla. State 0: Relatively straight; State 1: Somewhat laterally bent.

LOWER JAW

The pronounced modifications of the upper jaw of prochilodontids are paralleled by a significant revamping of the lower jaw, both in its overall, longitudinally foreshortened morphology and in details of the individual ossifications and associated soft tissues. These characters are discussed in the following sections by major jaw components.

Dentary

Various authors (e.g., Roberts, 1973b; Vari, 1983) have previously noted that the lower jaw of prochilodontids is distinctive in various features, most notably in being distinctly longitudinally shortened relative to the condition in other characiforms. That observation is confirmed by the comparisons in this study, and the foreshortening of the dentary is consequently hypothesized to be derived for the Prochilodontidae.

Prochilodontids also have a greatly expanded, laterally rotated trench that partially envelops the numerous series of small replacement teeth that are characteristic of the family. Typically, other characiforms have the replacement dentition for the outer row of dentary teeth situated in a trough or crypt internal to the dentary. Basal characiforms (Citharinidae, Distichodontidae) have a broad trough that is continuously open dorsally. A replacement tooth trench that is broadly open dorsally also occurs in the Anostomidae and Crenuchidae among groups towards the base of the phylogeny of the Characiformes as proposed by Buckup (1988, fig. 7). The lack of attached dentition anteriorly or throughout the lower jaw in the Curimatidae, Chilodontidae, Hemiodontidae, and Parodontidae, however, eliminates the need for an area in which replacement teeth develop, with an apparently correlated loss of the replacement tooth trench. Other groups of characiforms, in contrast, typically have the dentary replacement dentition enclosed within a bony crypt that is usually open dorsally via a series of small openings (the gubernacula, Shellis and Berkovitz, 1976:72) that are situated at the base of the functional teeth except when replacement teeth are in the process of shifting into functional position. During that process, those portions of the jaw are resorbed to permit passage of the replacement teeth into their functional position. Such nearly completely dorsally enclosed crypts for the dentary replacement trenches may represent a derived attribute for a major component of the Characiformes.

Examination of other clades within the Characiformes revealed only one other group, the members of the African family Citharinidae, particularly the species of *Citharidium* (Daget, 1962a, fig. 4; Vari, 1979:267), with a somewhat proportionally dorsally expanded and anteriorly rotated replacement tooth trench, albeit with these modifications not developed in the Citharinidae to the degree present in the Prochilodontidae. Notwithstanding the occurrence of somewhat similar dentary replacement trenches in both of these families, the trench in the Citharinidae is far less expansive than that characterizing the Prochilodontidae. Furthermore, numerous pronounced differ-

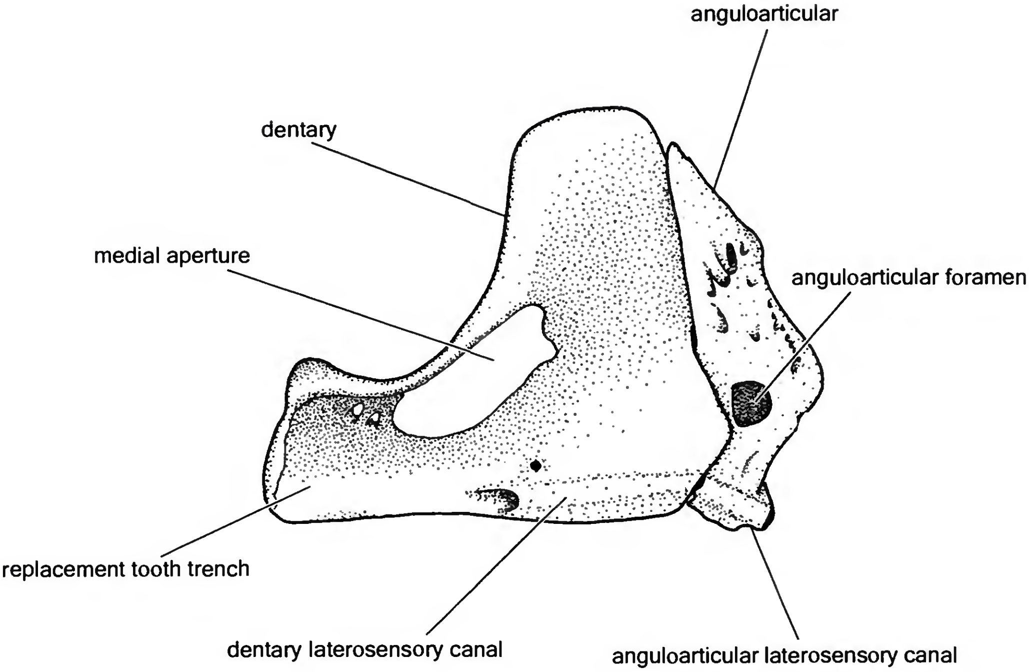


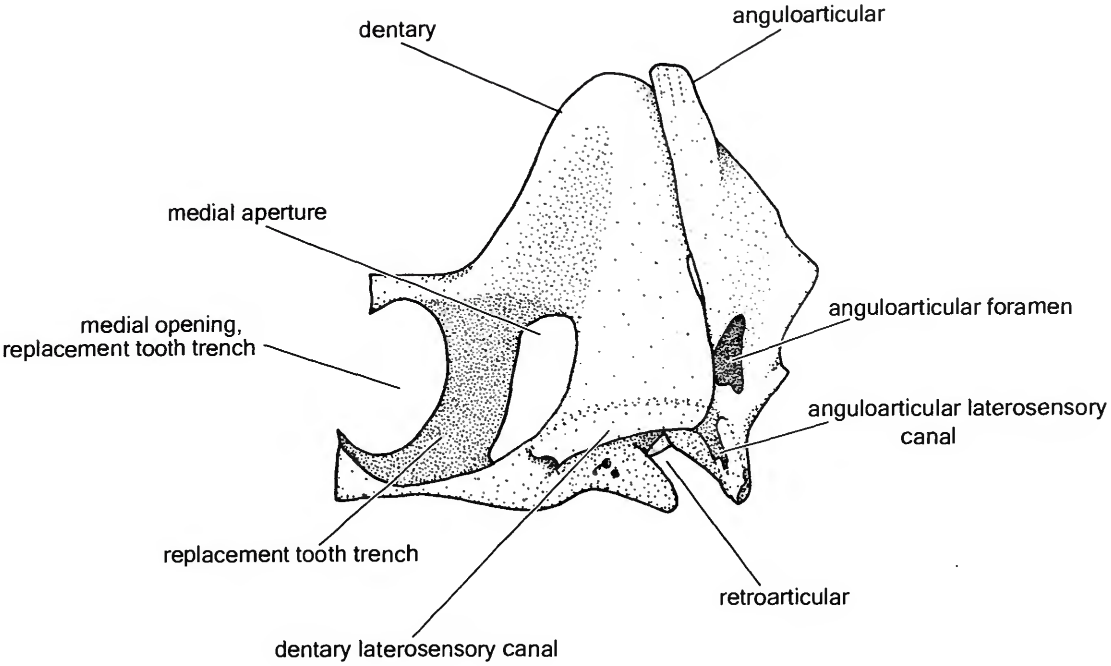
FIGURE 12.—*Prochilodus vimboides*, USNM 345752, bones of lower jaw, lateral view, anterior at left, dorsal at top.

ences exist in the overall morphology of all components of the lowers jaws in the Citharinidae versus the Prochilodontidae as evidenced by a comparison of Figures 12 and 13 herein with those of the lower jaws of *Citharidium* (Daget, 1962a, fig. 10) and *Citharinus* (Daget, 1962b, figs. 5, 7). Furthermore, the Citharinidae is most closely related to the Distichodontidae, and the clade formed by those families is, in turn, not closely related to the Prochilodontidae (Vari, 1979, 1983; Buckup, 1998). Thus, the expanded, anteriorly rotated trenches in the Citharinidae and Prochilodontidae are considered to be non-homologous with each other, and the broad dentary replacement tooth trench present in the Prochilodontidae is hypothesized to be a synapomorphy for the members of that family.

The degree of development of the anteriorly rotated dentary replacement tooth trenches differs in the three genera of the Prochilodontidae. Both *Prochilodus* (Figure 12) and *Semaprochilodus* have well-developed trenches whose anterior portions occupy approximately one-half of the vertical extent of the dentary in that region. In both of these genera, the contralateral trenches are consequently only continuous with each other to a limited degree across the dentary symphysis, with the continuity not apparent from a medial view (Figures 15, 16). In *Ichthyoelephas* (Figure 13), the anterior portion of the broader replacement tooth trench occupies almost the entire vertical extent of the dentary in the region proximate to the symphysis, with a resultant complete continuity of the contralateral trenches across the medially and massively developed dentary symphysis (Figure 17). Such massively developed replacement tooth trenches are unique to *Ichthyoelephas* among characiforms and are considered to be derived for the species of that genus.

CHARACTER 47. Form of dentary and dentary tooth replacement trench. State 0: Dentary not foreshortened and dentary replacement trench either absent or, if present, trench narrow and contralateral trenches not continuous across symphysis; State 1: Dentary foreshortened and dentary replacement tooth trench broad but with contralateral trenches continuous across symphysis only to limited degree; State 2: Dentary foreshortened and dentary replacement tooth trench very broad, with contralateral trenches almost completely continuous across symphysis.

The genera of the Prochilodontidae also demonstrate differences in the continuity of the ventral margin of the large medial aperture in the replacement tooth trench with the main body of the trench. In *Prochilodus* species (Figure 12), the ventral margin of the aperture is relatively smoothly continuous with the proximate, more ventrally situated portions of the bone. *Ichthyoelephas* and *Semaprochilodus*, in contrast, have a distinct ridge that extends along the ventral margin of the medial aperture in the dentary (ridge not apparent in the orientation of lower jaw illustrated in Figure 13). The absence of such a large aperture and associated ridge in the dentary among outgroups to the Prochilodontidae renders an a priori polarization of this feature impossible, and the outgroup condition is consequently



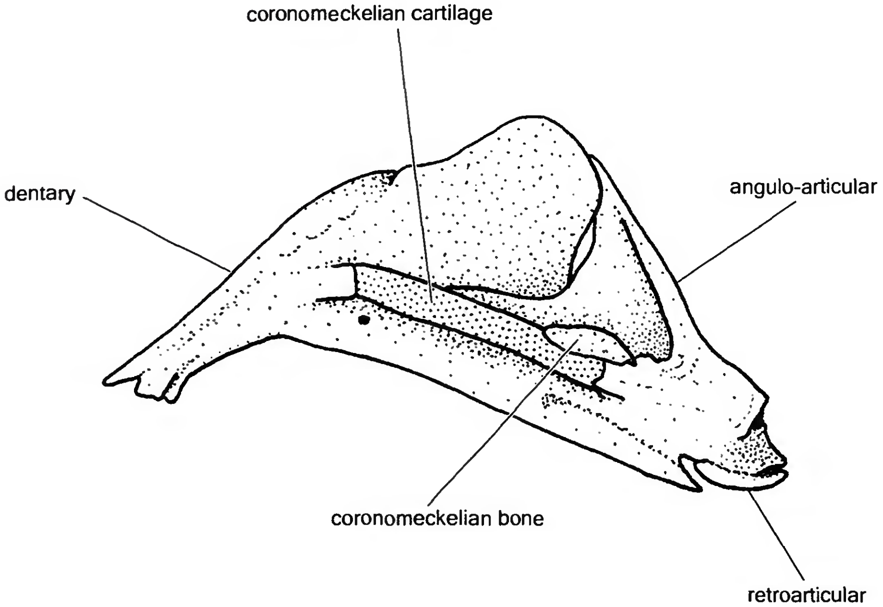


FIGURE 13 (above).—*Ichthyoelephas humeralis*, USNM 231437, bones of lower jaw, lateral view, anterior at left, dorsal at top.

FIGURE 14 (left).—*Potamorhina laticeps*, USNM 121325, bones of lower jaw, medial view, anterior at left, dorsal at top. (Dense patterned stippling represents cartilage.)

scored as unknown in the matrix. The presence of such a ridge on the dentary is optimized as being derived for *Ichthyoelephas* and *Semaprochilodus* under the overall most parsimonious hypothesis of relationships (see "Phylogenetic Reconstruction").

CHARACTER 48. Continuity between medial aperture in replacement tooth trench and main body of trench. State 0: Smoothly continuous; State 1: Not smoothly continuous, but with distinct intervening ridge along medial margin of aperture.

Contrary to the situation in other examined groups within the Characiformes, the posterior wall of the dentary replacement trench of the Prochilodontidae is perforated by a very large, horizontally elongate (*Prochilodus*, Figure 12, see also Miles, 1947, fig. 77, and *Semaprochilodus*) or rounded (*Ichthyoelephas*) aperture (round form of opening not apparent from lateral view as shown in Figure 13). This dentary aperture is subdivided into two portions in some specimens and is often preceded by several smaller foramina. A sheet of semi-transparent connective tissue extends across the primary aperture, so

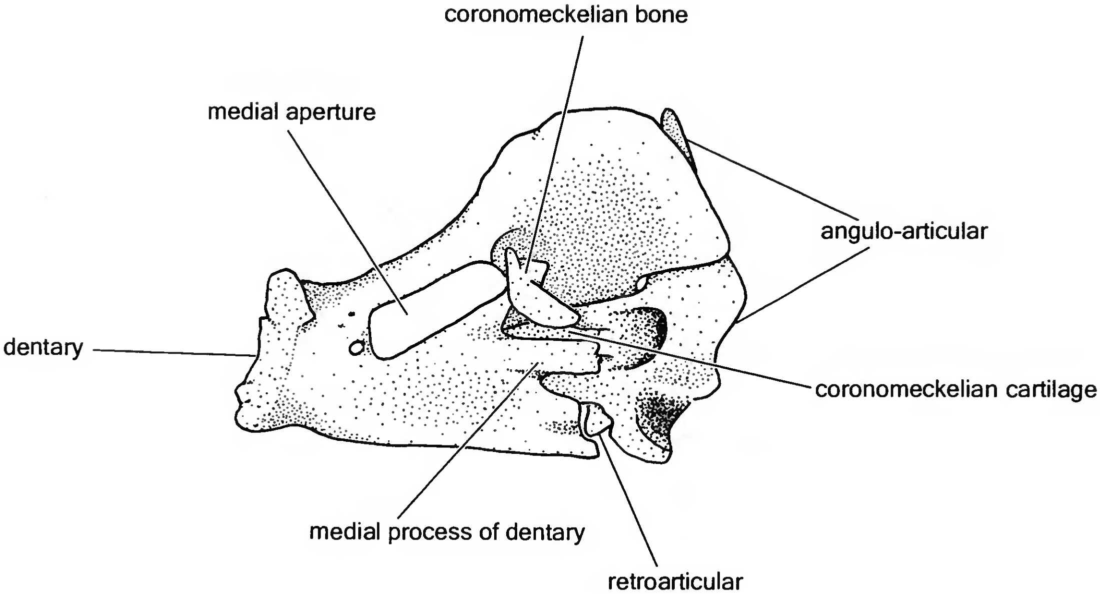


FIGURE 15.—*Prochilodus rubrotaeniatus,* USNM 225419, bones of lower jaw, medial view, anterior at left, dorsal at top. (Dense patterned stippling represents cartilage.)

that opening consequently does not serve as a passageway for muscles, nerves, or blood vessels.

Members of the Curimatidae, the first outgroup, and the Chilodontidae, a component of the second outgroup, with their respectively absent and reduced oral dentition, both lack dentary replacement tooth trenches or any indication of an aperture in the portion of the dentary that corresponds to the area perforated by the opening in the Prochilodontidae. The Anostomidae, the remaining component of the second outgroup, although having a second opening into the replacement tooth trench as does the Prochilodontidae, has that aperture located in the ventral rather than in the posterior portion of the replacement tooth chamber as in the latter family. Surveys of more distantly related outgroups to the Prochilodontidae similarly failed to find any other taxa in the Characiformes with an aperture into the dentary replacement trench comparable with that present in that family, and the possession of such an opening is hypothesized to be a synapomorphy for the species of the Prochilodontidae.

Vari (1983:49) subsumed the expansion of the dentary replacement tooth trench and the presence of the very large opening in the posterior wall of that trench into a single synapomorphy in his study that focused on the question of the higher level relationships of the Prochilodontidae. We instead recognize these features as separate characters herein in order to appropriately utilize the intrafamilial variation in these features in the phylogenetic analysis.

CHARACTER 49. Posterior wall of dentary replacement trench. State 0: Unperforated or with small perforations; State 1: With large, horizontally elongate or round opening.

A final character of note on the lateral portion of the dentary in the Prochilodontidae is the extent of the laterosensory canal segment in that bone. In all species of the Prochilodontidae, the laterosensory canal segment in the dentary is limited to the posterior one-half of that ossification (Figures 12, 13). This truncated condition differs markedly from the proportionally more elongate dentary canal segment present in the Curimatidae (e.g., *Curimatopsis microlepis* and *Curimatella alburna*, Vari, 1989a, fig. 39), the proximate sister group to the Prochilodontidae, and in many outgroup characiforms in which the canal extends anteriorly to a point much closer to the dentary symphysis. The truncate dentary laterosensory canal segment in the Prochilodontidae is considered to be derived.

CHARACTER 50. Extent of laterosensory canal segment in dentary. State 0: Extends from posterior portion of dentary into anterior one-half of that ossification; State 1: Limited to posterior one-half of dentary.

Turning to the ventral portion of the dentary, we find that the posteroventral corner of that bone in the members of the Prochilodontidae bears a distinct, posteroventrally directed, medially oriented process. This process of the dentary is apparently homologous with the posteroventral process of the dentary that extends ventral of, and is closely applied to, the anterior portion of the retroarticular in the Curimatidae (e.g., *Potamorhina laticeps,* see Vari, 1983, fig. 2d) and in many other groups in the Characiformes (e.g., *Brycon meeki;* see comments by Weitzman, 1962:33). The shift of this dentary process medially to varying degrees within the Prochilodontidae parallels the repositioning of the retroarticular onto the medial surface of the angulo-articular in that family (see comments under "Retroarticular," below). The somewhat elongate process on the posteroventral corner of the dentary in *Prochilodus* and *Semaprochilodus* is often not visible from a lateral view (Figure 12), whereas in the more compact lower jaw of *Ichthyoelephas* (Figure 13) this process assumes a more triangular form and is readily apparent. Regardless of its form, the possession of such a medially repositioned process on the posteroventral portion of the dentary is considered to be derived for the Prochilodontidae because of its absence in other examined characiforms.

CHARACTER 51. Orientation of process of dentary that extends along ventral surface of retroarticular. State 0: Posteriorly directed; State 1: Medially oriented.

The medial surface of the dentary also is replete with phylogenetically informative modifications within the Prochilodontidae. Whereas all examined outgroup characiforms have the coronomeckelian cartilage completely exposed along its medial surface (e.g., the curimatid *Potamorhina lacticeps,* Figure 14), the species of the Prochilodontidae have much of the medial surface of that cartilage overlapped by a well-developed, flattened, bony process that arises from the medial surface of the dentary approximately mid-way along the longitudinal extent of that ossification (Figures 15–17). Roberts (1973:218) noted the existence of this process of the dentary in prochilodontids, but his description of the structure applies only to the condition found in *Ichthyoelephas* in which the process is vertically oriented (Figure 17, see discussion below). In *Prochilodus* and *Semaprochilodus,* this ossified process of the dentary is anteroposteriorly elongate and extends directly posteriorly from the region where it arises from the main body of the dentary (Figures 15, 16). Regardless of its form, the medial process of the dentary that covers the ventral and, to varying degrees, medial surfaces of the coronomeckelian cartilage is unique to, and apomorphic for, the members of the Prochilodontidae.

CHARACTER 52. Medial surface of coronomeckelian cartilage. State 0: Not covered by medial process of dentary; State 1: At least partially covered by medial process of dentary.

Ichthyoelephas has the bony process that overlies the coronomeckelian cartilage in the highly modified dentary of that genus realigned into an almost vertical orientation (Figure 17) rather than the horizontal alignment present in *Prochilodus* (Figure 15) and *Semaprochilodus* (Figure 16). The process not only overlaps a major portion of the coronomeckelian cartilage medially, but it also continues beyond the dorsal limit of that cartilage to articulate via an articular surface with the ventral portion of the coronomeckelian bone. It is impossible, however, to a priori polarize the two forms of the process (horizontally versus vertically oriented) within the Prochilodontidae because of the absence of the structure in characiform outgroups, so the process is coded as unknown in the outgroup. The optimization under the final most parsimonious hypothesis of intrafamilial relationships indicates that the condition in *Ichthyoelephas* is derived (see "Phylogenetic Reconstruction").

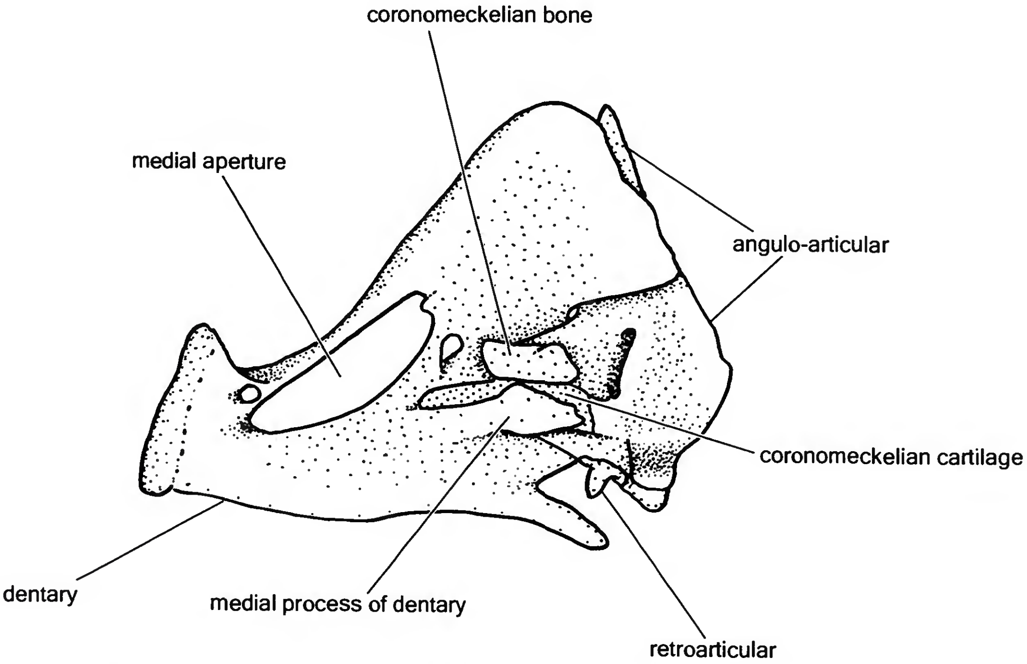


FIGURE 16.—*Semaprochilodus insignis,* USNM 290148, bones of lower jaw, medial view, anterior at left, dorsal at top. (Dense patterned stippling represents cartilage.)

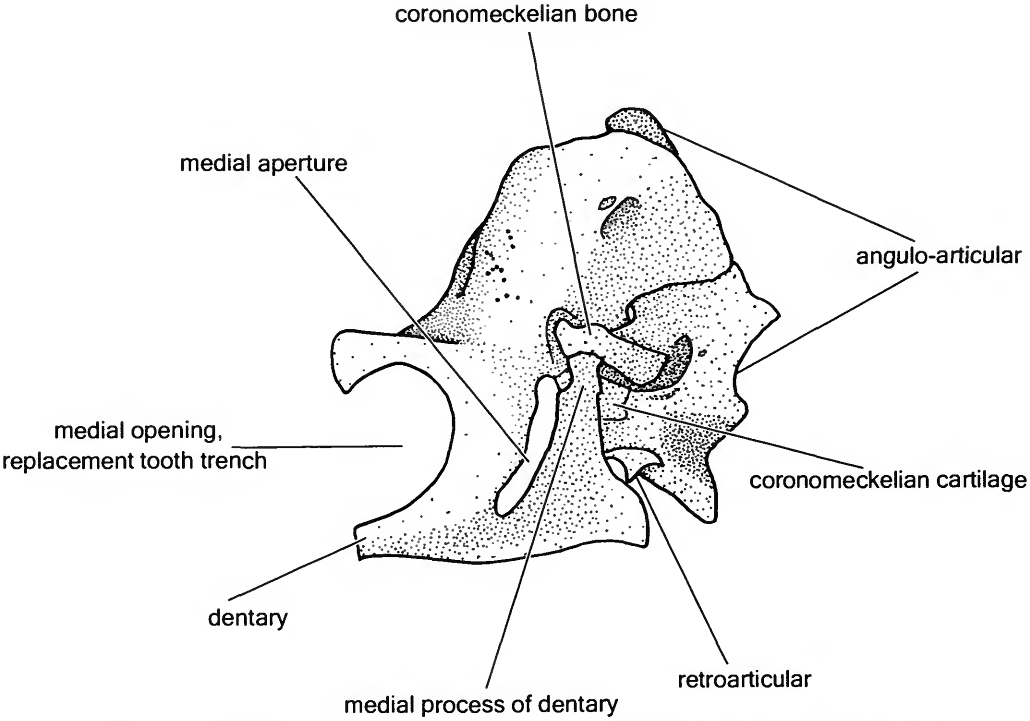


FIGURE 17.—*Ichthyoelephas humeralis,* USNM 231437, bones of lower jaw, medial view, anterior at left, dorsal at top. (Dense patterned stippling represents cartilage.)

CHARACTER 53. Form and orientation of medial process of dentary that overlaps coronomeckelian cartilage. State 0: Anteroposteriorly elongate and horizontally aligned but not in contact with coronomeckelian bone; State 1: More compact and vertically aligned and in contact with ventral portion of coronomeckelian bone.

Coronomeckelian Bone

The second suite of features of note on the medial surface of the lower jaw involves restructurings of the form of the coronomeckelian bone. Characiforms, including the first outgroup to the Prochilodontidae, the Curimatidae, usually have a relatively straight, horizontally elongate coronomeckelian ossification that has a relatively posterior position along, or proximate to, the vertical through the point where the angulo-articular passes lateral to the posterodorsal portion of the dentary. Within the Prochilodontidae, *Semaprochilodus* species have a coronomeckelian bone that most closely approximates the form of the bone typical of outgroup characiforms. *Prochilodus* and *Ichthyoelephas* have distinct but divergent modifications of the coronomeckelian bone, with *Prochilodus* species differing further in having the ossification repositioned relative to the form of the bone in other characiforms.

In *Prochilodus* species, the posterior portion of the coronomeckelian bone retains its plesiomorphic horizontal orientation, but the anterior section of that ossification is anterodorsally or dorsally oriented, with the two sections of the ossification meeting at a distinct angle (Figure 14). Some *Prochilodus* species have the restructuring pronounced to such a degree that the coronomeckelian bone of the left lower jaw has the form of a backward L from a medial view. Furthermore, the coronomeckelian bone in *Prochilodus* species is shifted distinctly anteriorly relative to the condition in outgroups such that the posterior limit of that ossification is positioned distinctly anterior of the vertical through the point where the vertical portion of the angulo-articular passes lateral of the posterodorsal portion of the dentary. This restructuring and repositioning of the coronomeckelian bone in the species of *Prochilodus* is a uniquely derived modification that is synapomorphic for members of the genus.

CHARACTER 54. Longitudinal morphology and position of coronomeckelian bone. State 0: Relatively anteroposteriorly straight and situated along, or proximate to, the vertical through the point where the angulo-articular passes lateral to the posterodorsal portion of the dentary; State 1: With distinct angle in coronomeckelian bone and anterior section of ossification oriented dorsally or anterodorsally and with posterior terminus of bone located distinctly anterior of vertical through the point where the angulo-articular passes lateral to the posterodorsal portion of the dentary.

The mode of restructuring of the coronomeckelian bone in the remaining component of the Prochilodontidae, the species of *Ichthyoelephas,* is striking. Rather than being relatively anteroposteriorly flat when viewed medially, as is its morphology in the majority of characiforms, the coronomeckelian bone in *Ichthyoelephas* is distinctly convex and matches the form of the proximate portions of the dentary and angulo-articular. Furthermore, the coronomeckelian bone of *Ichthyoelephas* species is positioned in a distinct depression on the medial surface of the dentary and has a ventral articular surface that contacts the corresponding articular surface on the dorsally directed process of the medial surface of the dentary (see description of latter process, above). These features are absent both in the other genera of the Prochilodontidae and among examined outgroups; therefore, this form of the coronomeckelian bone is considered to be synapomorphic for the species of *Ichthyoelephas.*

CHARACTER 55. Form of the coronomeckelian bone. State 0: Not as in State 1; State 1: Distinctly concave from medial view and positioned in depression on medial surface of dentary and angulo-articular and with ventral articular surface that contacts dorsal surface of dorsally directed medial process on dentary.

Angulo-articular

The laterosensory canal segment in the angulo-articular in proximate outgroups to the Prochilodontidae is longitudinally aligned and continues the axis of the laterosensory canal segment that extends through the dentary. A comparable orientation of the laterosensory canal system in the angulo-articular occurs in the Curimatidae (e.g., *Potamorhina laticeps,* Vari, 1983, fig. 2d), the Chilodontidae, and among more generalized members of the Anostomidae (e.g., *Leporinus*). Such an alignment of this canal segment in the angulo-articular also occurs in various other groups in the Characiformes, including basal families such as the Distichodontidae (*Xenocharax,* Daget, 1960, fig. 7) and Citharinidae (*Citharidium,* Daget, 1962a, fig. 10); therefore, it is considered to be the plesiomorphic condition within the order. In the Prochilodontidae, the laterosensory canal segment in the angulo-articular is instead anterodorsally oriented and is aligned at a distinctly more acute angle relative to the axis of the canal in the dentary (Figures 12, 13); this is hypothesized to be a derived condition.

CHARACTER 56. Alignment of laterosensory canal segment in angulo-articular. State 0: Longitudinally aligned and continues along axis of laterosensory canal segment in dentary; State 1: Anterodorsally aligned and at distinct angle to axis of laterosensory canal segment in dentary.

The association of the dorsal portion of the angulo-articular to the adjoining posterodorsal region of the dentary in the Prochilodontidae is unique among examined taxa in the Characiformes. All members of the Prochilodontidae have a distinct separation of the dorsal portion of the angulo-articular and the adjoining region of the dentary, with the gap most pronounced in the anterodorsal portion of the region of overlap (Figures 12, 13, 15–17). The resultant intervening space between the angulo-articular and dentary is filled with a dense connective tissue mass that is continuous dorsally with the connective tissue pad situated at the posterodorsal margin of the lower jaw in prochilodontids.

In almost all other members of the Characiformes, the opposing surfaces of these bones are tightly applied to each other. The single exception to this typical outgroup characiform condition is the condition in a clade within the Old World family Distichodontidae that consists of *Belonophago, Distichodus, Eugnatichthys, Hemigrammocharax, Hemistichodus, Ichthyborus, Mesoborus, Microstomatichthyoborus, Nannocharax, Paraphago,* and *Phago.* These genera are characterized by mobility between the otherwise closely applied angulo-articular and the dentary (see discussion in Vari, 1979:269), but they lack an intervening dense connective tissue mass between the angulo-articular and dentary. Basal lineages within the Distichodontidae (*Xenocharax, Neolebias, Nannaethiops, Paradistichodus*) retain a tight association between the angulo-articular and the dentary, as do the members of the Citharinidae, the sister group to the Distichodontidae (Vari, 1979). Consequently, a tight junction of the angulo-articular and the dentary is considered to be plesiomorphic for the Distichodontidae. This plesiomorphic condition supports the hypothesis that the Distichodontidae is not closely related to the Prochilodontidae (Vari, 1979, Buckup, 1998). Given that phylogenetic information and the unique form of the gap between the dorsal portion of the angulo-articular and the adjoining regions of the dentary in the Prochilodontidae, this adaptation in the latter family is considered to be derived.

CHARACTER 57. Association of dorsal portion of angulo-articular and adjoining surface of dentary. State 0: Dorsal portion of angulo-articular in close contact with dentary; State 1: Dorsal portion of angulo-articular separate from adjoining portion of dentary, with intervening space occupied by dense connective tissue mass.

A final character of phylogenetic significance in the angulo-articular of the Prochilodontidae discovered during this study is the presence of a large foramen on the lateral surface of the bone in the region anterodorsal of the articular facet (Figures 12, 13). This lateral opening is continuous with a cavity in the central portion of the angulo-articular. That cavity, in turn, has a well-developed opening onto the medial surface of the bone (Figures 15–17). Openings on the lateral surface of the angulo-articular in the region occupied by the aperture occur in the Prochilodontidae as well as in various other taxa within the Characiformes; however, in none of the examined outgroups are the apertures proportionally as extensive as those in the Prochilodontidae. The condition in the Prochilodontidae is consequently considered to be derived.

CHARACTER 58. Large foramen in angulo-articular anterodorsal of articular facet. State 0: Absent; State 1: Present.

Retroarticular

As noted by Vari (1983:11), the retroarticular in the Prochilodontidae is proportionally significantly smaller than it is in other characiforms. Furthermore, the prochilodontid retroarticular has a somewhat laterally concave form, a morphology unknown elsewhere within the Characiformes. Moreover, the ossification in the Prochilodontidae is distinctive in being repositioned to the anteromedial surface of the angulo-articular; as a consequence, it is barely, if at all, visible from lateral view (Figures 12, 13). These conditions are unknown elsewhere in the Characiformes. Because of the unique nature of the form and position of the retroarticular of the Prochilodontidae within the Characiformes, these restructurings of the retroarticular are considered to be derived.

CHARACTER 59. Form and position of retroarticular. State 0: Proportionally moderate in size, with laterally flat or slightly convex form and positioned on ventrolateral region of angulo-articular; State 1: Proportionally relatively small with laterally concave form and positioned on anteromedial surface of angulo-articular.

Intrafamilial variation in the association of the retroarticular with the angulo-articular also is phylogenetically informative. In both *Ichthyoelephas* and *Semaprochilodus*, the retroarticular, albeit closely applied to the anteroventral surface of the angulo-articular, can be readily distinguished from the latter ossification. Species of *Prochilodus*, in contrast, have the association between the retroarticular and angulo-articular significantly tighter than elsewhere in either the Prochilodontidae or proximate outgroups. The close association of these elements renders it difficult, and sometimes impossible, to delimit the boundaries of the retroarticular relative to those of the angulo-articular even in cleared and stained specimens of *Prochilodus* species, and this is considered to be a derived condition.

CHARACTER 60. Association of retroarticular with angulo-articular. State 0: Retroarticular closely applied to angulo-articular, but bones readily distinguishable; State 1: Retroarticular very tightly associated with angulo-articular, with boundaries of retroarticular difficult to discern.

PRIMORDIAL LIGAMENT

The A_1 portion of the adductor mandibulae in prochilodontids extends anteriorly from the lateral surface of the vertical and horizontal limbs of the preopercle to an attachment on the posterior margin of the lower jaw and onto a tendonous band that extends from the posterior portions of the lower jaw anterodorsally to the maxilla. This tendonous band, the primordial ligament (Winterbottom, 1974:232; the articular-premaxillary ligament of Alexander, 1964:183) has diverse areas of attachment onto the maxilla throughout the Characiformes. Basal groups within the order, such as *Xenocharax* (Distichodontidae) and *Citharinus* (Citharinidae), have the attachment of the ligament onto the dorsal portions of the maxilla (Vari, 1979a, figs. 39, 41). This pattern also is found in some more-derived taxa, such as *Brycon* (Characidae). Among proximate groups to the Prochilodontidae, all members of the Curimatidae, except for the species of *Curimatopsis*, have the attachment of the ligament on the medial surface of the maxilla (see Vari, 1989a, fig. 37). Species of *Curimatopsis* have the attachment situated on the posterior margin of the maxilla (Vari, 1989a:40). An attachment of the primordial ligament onto the medial surface of the maxilla similarly occurs in all examined taxa of the Anostomidae and Chilodontidae, which together constitute the secondary outgroup to the Prochilodontidae. In these proximate outgroups to the Prochilodontidae, the attachment of the ligament is situated on the dorsal or sometimes the middle regions of the maxilla, and that ossification either lacks bony elaborations at the site of attachment of the ligament or, at most, has a small ridge on the maxilla that presumably serves to increase the surface area for attachment of the ligament. The species of the Prochilodontidae, in contrast, have the attachment of the primordial ligament onto the anteromedial margin, rather than the medial or posterior margins of the maxilla. Furthermore, the portion of the maxilla onto which the ligament attaches is significantly anteriorly expanded into a three-dimensionally complex lever-like structure that extends from the main body of the ossification (Figure 10, see also description under "Maxilla," above). Such an anterior position of the attachment of the primordial ligament onto the maxilla has not been encountered elsewhere within the examined taxa of the Characiformes, and the area of the attachment in the Prochilodontidae is consequently hypothesized to be derived.

CHARACTER 61. Area of attachment of primordial ligament onto maxilla. State 0: Attachment onto dorsal or medial surface of maxilla either directly to main body of bone or to small ridge that arises from ossification; State 1: Attachment onto anteromedially situated, highly developed, distinct, lever-like process of maxilla.

INFRAORBITAL SERIES

First Infraorbital

Prochilodontids demonstrate various modifications of the morphology of the first infraorbital, the most obvious of which is the degree of development of the anterior portion of the bone. In members of the Characiformes, the first infraorbital-typically has the form of a relatively flat ossification that extends varying distances anterior of the vertical through the anterior margin of the orbit (e.g., *Brycon meeki*, Weitzman, 1962, fig. 8). In the clade formed by the Prochilodontidae, Curimatidae, Anostomidae, and Chilodontidae the first infraorbital typically extends distinctly forward of the anterior margin of the orbit, but in three of these families, the Curimatidae (e.g.,

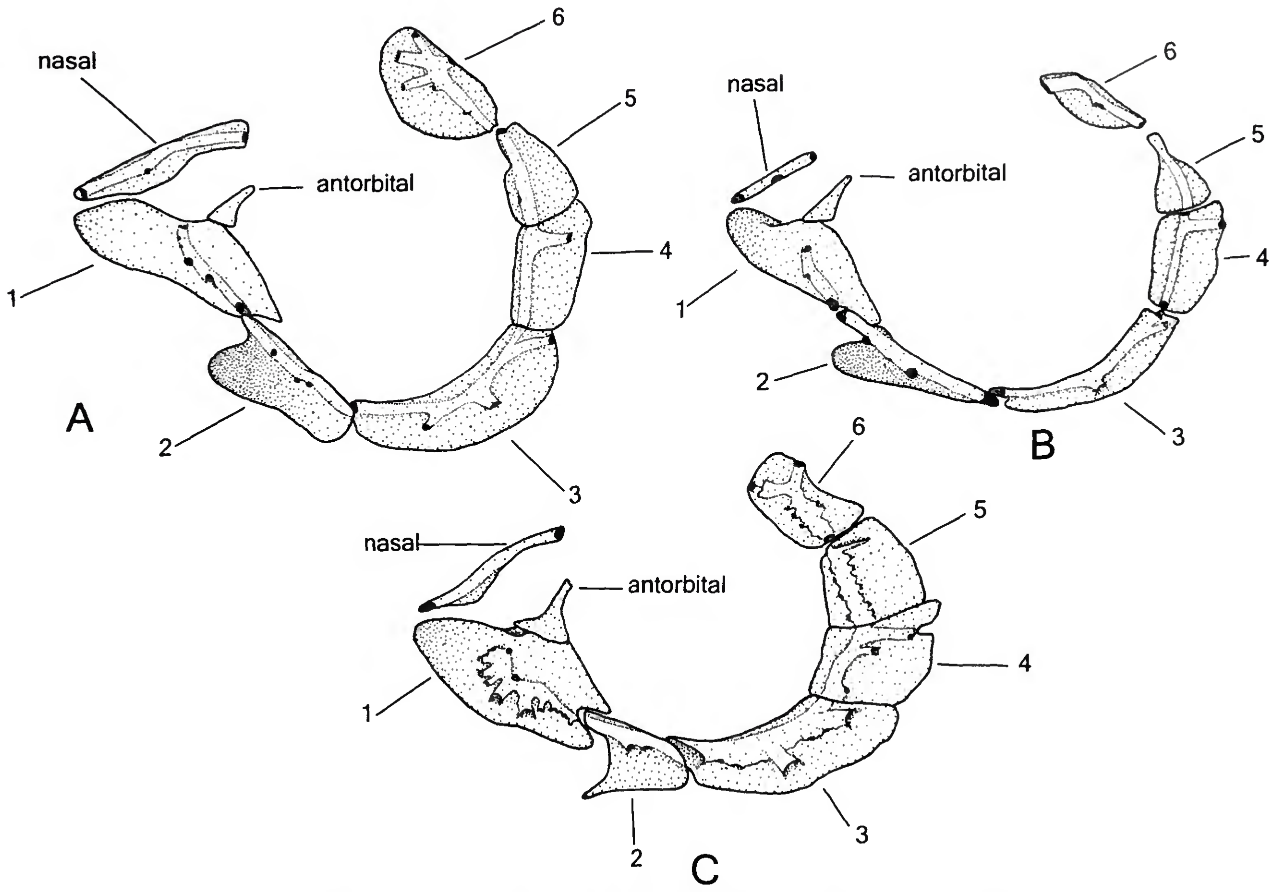


FIGURE 18.—Nasal, antorbital, and infraorbital bones and primary associated laterosensory canal segments: A, *Prochilodus argenteus,* MZUSP 42718; B, *Semaprochilodus brama,* MZUSP 21254; C, *Ichthyoelephas humeralis,* USNM 290374; left side, lateral view. Small ramifying canals in first infraorbital not illustrated.

Curimata macrops, Roberts, 1973b, fig. 15), Anostomidae (e.g., *Schizodon fasciatus,* Roberts, 1973b, fig. 18), and Chilodontidae, the anterodorsal portion of the infraorbital remains distinctly separated from the anteroventral margin of the nasal bone. In contrast, the Prochilodontidae has the anterior portion of the first infraorbital proportionally significantly larger than in its proximate sister groups, with the anterior expansion reflected by the proximity (Figure 18) or, in large specimens, the contact of the anterodorsal portion of the first infraorbital with the ventral margin of the nasal. This condition is hypothesized to be derived in light of the morphology of the first infraorbital in outgroups.

The Prochilodontidae also differs from proximate groups within the Characiformes in the three-dimensional architecture of the first infraorbital. Members of the Curimatidae, Anostomidae, and Chilodontidae have transversely relatively flat first infraorbitals without pronounced elaborations present on the medial surface of the bone. Genera of the Prochilodontidae, however, have a pronounced medial curvature of the anterior portion of the ossification to match the contour of the snout in that region. Equally striking is the presence in the Prochilodontidae of a distinct medial ridge along the dorsomedial portion of the first infraorbital, with the ridge apparently contributing to the support of the floor of the nasal capsule. An elongate, anteriorly curving infraorbital with a medial ridge on its dorsomedial portion has not been encountered in examined outgroup characiforms, and its occurrence is hypothesized to be a synapomorphy for the species of the Prochilodontidae.

CHARACTER 62. Relative extent of the anterior portion of the first infraorbital and overall form of that bone. State 0: Anterior margin of first infraorbital falls distinctly short of ventral margin of nasal and overall form of first infraorbital relatively flat and without ridge on medial surface of bone; State 1: Anterior margin of first infraorbital approaches or contacts ventral surface of nasal, and first infraorbital medially curved with distinct ridge on medial surface of bone.

The morphology of the segment of the laterosensory canal system in the first infraorbital varies within the Prochilodontidae. When present, this canal segment in examined characiforms, including the Curimatidae, Anostomidae, and Chilodontidae (see Vari, 1995, fig. 1), is typically a relatively simple tube that terminates anterodorsally approximately at the vertical that passes through the area of contact of the antorbital with the first infraorbital. In all members of the Prochilodontidae, there are a series of ramifying smaller channels that extend anteriorly from the main body of the laterosensory canal into the anteriorly elongate portion of the first infraorbital. These ramifications are moderately developed in *Ichthyoelephas* and *Semaprochilodus* and most highly developed in *Prochilodus*, an apparent further derived condition (note: ramifying canals not shown in Figure 18A–C). Because of their small size and irregular pattern, it is unclear whether these smaller channels in the first infraorbital of prochilodontids function as part of the laterosensory canal system.

CHARACTER 63. Series of small, ramifying canals that extend off main body of laterosensory canal in first infraorbital. State 0: Absent; State 1: Present and moderately developed; State 2: Present and highly developed.

Several further modifications of the first infraorbital are phylogenetically informative at subfamilial levels. In *Ichthyoelephas*, the posterior portion of the first infraorbital is deeply indented to accommodate the anterodorsal tubular portion of the second infraorbital (Figure 18C). A comparable indentation on the first infraorbital is absent in *Prochilodus* (Figure 18A), *Semaprochilodus* (Figure 18B), and proximate outgroups to the Prochilodontidae (Curimatidae, see Roberts, 1973b, fig. 15; Chilodontidae, see Vari et al., 1995, fig. 1; Anostomidae, see Winterbottom, 1980, figs. 30–32). Consequently, the possession of an indented first infraorbital is hypothesized to be derived for *Ichthyoelephas*.

CHARACTER 64. Form of posterior portion of first infraorbital. State 0: Not indented; State 1: Deeply indented.

The primary portion of the laterosensory canal system in the first infraorbital in *Prochilodus* (Figure 18A) and *Semaprochilodus* (Figure 18B) is a relatively straight tube with three or four openings, one at each end of the canal segment and one or two apertures along the anteroventral border of the canal. A single examined specimen of *P. britskii* has one of these openings located at the end of a short secondary tube, a possible autapomorphy for the species, but it may be a function of the relatively large size of the specimen in question relative to the other cleared and stained *Prochilodus* specimens examined in this study. The species of *Ichthyoelephas* (Figure 18C) have a much more elaborate pattern of openings in the first infraorbital that consist of three to five primary apertures and various smaller secondary channels that extend from the ventral border of the canal. Such a more elaborate pattern of the laterosensory canal is already present in medium-sized cleared and stained specimens of *I. humeralis* but is particularly pronounced in larger individuals of that species and in the large cleared and stained specimen of *I. longirostris* examined for this study. In light of the absence of this elaborate form of the laterosensory canal system in the first infraorbital in the other genera of the Prochilodontidae and in the sister group to that family, the Curimatidae, the possession of such a canal system in *Ichthyoelephas* is hypothesized to be derived.

CHARACTER 65. Form of primary laterosensory tube in first infraorbital. State 0: Tube relatively straight and with four or five openings; State 1: Tube with series of secondary canals and multiple openings.

Second Infraorbital

The overall form of the second infraorbital is the most obvious derived attribute of that ossification in the Prochilodontidae. All species of the family have a distinct indentation on the anterior portion of the second infraorbital (Figure 18A–C). This indentation of the second infraorbital is bordered ventrally by an anteroventrally directed process that extends below the posteroventral margin of the fleshy lips, a feature commented upon previously by various authors (Roberts, 1973b:219; Vari, 1983:33). The second infraorbital in the Curimatidae (e.g., *Acuticurimata* (=*Curimata*) *macrops*, see Roberts, 1973, fig. 15), Anostomidae (e.g., *Anostomus spiloclistron*, Winterbottom, 1980, fig. 31), and Chilodontidae (e.g., *Caenotropus labyrinthicus*, see Vari et al., 1995, fig. 1), which are the proximate outgroups to the Prochilodontidae, in contrast, retains the straight or convex ventral margin typical for many characiforms. Furthermore, whereas basal groups in the Curimatidae (*Curimatopsis*, *Potamorhina*) and other outgroups have a distinct separation between the anteroventral margin of the second infraorbital and the anterior portion of the laterosensory canal segment in that bone, in the Prochilodontidae that portion of the laterosensory canal system delimits the border of the anterodorsal portion of the bone (Figure 18A–C). Thus, it would appear that the indentation along the anterior margin of the second infraorbital in the Prochilodontidae is a consequence of the elimination of a portion of that bone to accommodate the expanded fleshy lips characteristic of the family rather than the development of an anteroventral extension on the ossification. Further evidence for this assumption comes from the fact that the anterior limit of the anterodorsal portion of the second infraorbital and the anterior limit of the anteroventral process on that bone lie approximately along the same vertical line, the arrangement in proximate outgroups to the family. The distinct indentation on the second infraorbital, a feature unknown elsewhere in characiforms, was previously proposed as a synapomorphy for the Prochilodontidae by Vari (1983:33), who examined a subset of the species of the family. That conclusion is supported by the more encompassing analysis in this study.

The second infraorbital of *Ichthyoelephas* (Figure 18C) has the pronounced anteroventral evacuation of the anterior margin of the bone developed beyond the morphology found in both

Prochilodus (Figure 18A) and *Semaprochilodus* (Figure 18B). This restructuring, which accommodates the particularly large lips characteristic of the genus, results in an acute triangular anteroventral process on the second infraorbital that is unknown elsewhere among characiforms, and this acute shape is considered to be a further derived attribute.

CHARACTER 66. Overall form of second infraorbital. State 0: Without distinct indentation on anterior portion; State 1: With indentation on anterior portion moderately to very well developed; State 2: With indentation on anterior portion very well developed and with acutely triangular anteroventral process.

The second infraorbital in the Prochilodontidae also is more three dimensionally complex than it is elsewhere within the Characiformes. In other members of the order, the second infraorbital is typically relatively flat parasagittally (e.g., Chilodontidae, Vari et al., 1995, fig. 1). The ventral margin of the second infraorbital, which often contacts or approximates the lateral margin of the quadrate in characiforms, is, in turn, situated approximately in the same parasagittal plane as the dorsal portion of that infraorbital. In the Prochilodontidae, in contrast, the dorsal portion of the second infraorbital is shifted laterally relative to the main body of the bone, apparently as a consequence of the restructuring of that region of the head to accommodate the enlarged lips and highly modified, posterodorsally repositioned upper jaw. Among the most notable of the many alterations is the enlargement and posterodorsal repositioning of the distal portion of the maxilla. This change in the position of the maxilla is accommodated by a lateral shift of the entire first infraorbital and the anterior portion of the second infraorbital. Continuity between the laterosensory canal segments of the first and second infraorbitals in the laterally repositioned anterior portion of the infraorbital series is maintained by the lateral shift of the laterosensory canal-bearing portion of the second infraorbital. The canal consequently extends through a distinct dorsolateral process on the second infraorbital in *Prochilodus* (Figure 18A) and *Semaprochilodus* (Figure 18B), with the process further modified in *Ichthyoelephas* (see comments below with respect to restructuring of this element in *Ichthyoelephas*). As a consequence, the plate-like ventral portion of the second infraorbital in *Prochilodus* and *Semaprochilodus* is located in a plane distinctly medial to that of the dorsal canal-bearing portion of the bone.

Ichthyoelephas has the lateral process along the ventral margin of the quadrate proportionally further developed laterally than in *Prochilodus* and *Semaprochilodus*. This lateral extension of the lateral process of the quadrate in *Ichthyoelephas* provides an increased attachment area on that bone for the notably enlarged adductor mandibulae muscles. The expanded muscles are apparently associated with the extremely large lips characteristic of the species of that genus. Both the expansion of the adductor mandibulae muscles and the lateral extension of the ventrolateral process of the quadrate are accommodated by a lateral shift of the ventral portion of the second infraorbital. This restructuring of the second infraorbital results in a reduction in the degree of separation of the parasagittal planes that extend through the dorsal and ventral portions of that bone in the species of *Ichthyoelephas* (Figure 18C) in comparison with the morphology of the bone in *Prochilodus* or *Semaprochilodus*. At first appraisal the condition in *Ichthyoelephas* approximates the primitive form of the second infraorbital found in characiform outgroups in being relatively flat along its lateral surface; however, the condition of the second infraorbital in *Ichthyoelephas* differs from the form of that ossification in nonprochilodontid characiforms in retaining the distinct dorsal canal-bearing process, which is present also in *Prochilodus* and *Semaprochilodus*. Furthermore, in *Ichthyoelephas* this process is situated on the medial surface of the bone as a consequence of the lateral shift of the ventral portion of the ossification, whereas in *Prochilodus* and *Semaprochilodus* it is positioned on the lateral surface of the ossifications.

CHARACTER 67. Three dimensional morphology of second infraorbital. State 0: Without distinct process that carries laterosensory canal segment in anterior of bone; State 1: With distinct process that carries laterosensory canal segment in anterior of bone.

Third Infraorbital

The third infraorbital in the Curimatidae (e.g., *Acuticurimata* (=*Curimata*) *macrops*, see Roberts, 1973b, fig. 15), Anostomidae (e.g., *Pseudanos trimaculatus*, see Winterbottom, 1980, fig. 30), and Chilodontidae (e.g., *Chilodus punctatus*, see Vari et al., 1995, fig. 1), the proximate outgroups to the Prochilodontidae, has the form of a moderately wide, plate-like ossification with a relatively simple laterosensory canal system that runs through the dorsal portion of the ossification and with ventrally or posteroventrally directed side branches of the primary canal that are either absent or very abbreviated. Various modifications of the overall form of the third infraorbital and of the associated laterosensory canal system characterize the Prochilodontidae and its subunits.

Prochilodontids are all characterized by the possession of various combinations of distinct anteroventral, ventral, and posteroventral branches of the laterosensory canal system that extend varying extents toward the ventral margin of the third infraorbital. The simplest form of these elaborations within the Prochilodontidae occurs in *Ichthyoelephas* and *Semaprochilodus*, which have two major branches that arise from the ventral margin of the primary canal in the third infraorbital (Figure 18C). A more complex form occurs in the species of *Prochilodus*, which have three or four branches that extend from the ventral margin of the primary canal system in the third infraorbital (Figure 18A). The presence of the additional two to four branches that arise from the ventral margin of the laterosensory canal system in the third infraorbital is considered to be a synapomorphy for the Prochilodontidae. The more elaborate pattern of three or four ventral branches off the main laterosensory canal in the third infraorbital is, in turn, hypothesized to be synapomorphic for the species of *Prochilodus*.

CHARACTER 68. Form of laterosensory canal system in dorsal portion of third infraorbital. State 0: Relatively simple, without series of secondary canals that arise from ventral margin of primary canal; State 1: With two secondary canals that arise from ventral margin of primary canal; State 2: With three or four secondary canals that arise from ventral margin of primary canal.

The species of *Semaprochilodus* (Figure 18B) also differ from the remaining genera of the family (Figure 18A,C) and from proximate outgroups to the Prochilodontidae (see citations in previous section) in having a relatively narrow third infraorbital that covers only a reduced portion of the cheek musculature laterally. Such a narrow third infraorbital is considered to be derived based upon its absence in proximate outgroups.

CHARACTER 69. Relative size of third infraorbital. State 0: Wide; State 1: Narrow.

Fourth Infraorbital

The fourth infraorbital in the Prochilodontidae and proximate outgroups to that family typically has an approximately posteriorly directed side branch that extends varying distances from the primary laterosensory canal segment, with the posterior margin of the ossification being almost straight and terminating at the rear of the main body of the bone (see Vari, 1989a, fig. 35, for conditions in the Curimatidae). Only two derived conditions can be unambiguously identified within the intrafamilial variation in the form of the posterior side branch of the canal.

Three species of *Semaprochilodus* (*S. insignis*, *S. kneri*, *S. taeniurus*) have the portion of the fourth infraorbital that carries the posterior segment of the laterosensory canal posteriorly expanded as a bony tube that continues beyond the rear margin of the adjoining portions of the bone. The only occurrence of this modification in examined proximate outgroups is in the species of the curimatid genus *Potamorhina* (see Vari, 1989a, fig. 35). The common occurrence of this character in a subunit of *Semaprochilodus* and in one genus in the Curimatidae is most parsimoniously hypothesized to be convergent in light of the numerous synapomorphies for the Curimatidae and the clade within that family that includes *Potamorhina* (Vari, 1989a, fig. 44) and given the overall phylogenetic evidence presented herein as to the monophyly of the Prochilodontidae. The presence of the posterior expansion of the fourth infraorbital in these three *Semaprochilodus* species is consequently hypothesized to be derived.

CHARACTER 70. Degree of development of posteriorly directed branch of laterosensory canal in fourth infraorbital. State 0: Branch terminates at, or anterior of, posterior margin of bone; State 1: Branch extends as bony tube beyond posterior margin of bone.

The two species of *Ichthyoelephas* have a condition of the fourth infraorbital diametrically opposite to that in the noted *Semaprochilodus* species. Both of those species have a distinct notch situated along the posterior portion of the fourth infraorbital in the region where the posterior laterosensory canal segment contacts the rear of that ossification (Figure 18C); this is an alternative derived morphology and one that is absent elsewhere in the Prochilodontidae (Figure 18A,C) and proximate outgroups.

CHARACTER 71. Posterior margin of fourth infraorbital. State 0: Approximately straight; State 1: With distinct notch at level of posterior branch of laterosensory canal.

Fifth Infraorbital

The dorsal region of the fifth infraorbital in both *Ichthyoelephas* and *Prochilodus* is distinctly wider than the associated portion of the enclosed laterosensory canal segment, and a plate-like main body of the ossification extends to the dorsal margin of the bone (Figure 18A,C). The dorsal opening of the sensory canal in the fifth infraorbital in both of these genera also lies immediately proximate to the ventral opening into the laterosensory canal segment in the sixth infraorbital. *Semaprochilodus* species, in contrast, have the dorsal portion of the fifth infraorbital either reduced to a bony tube that envelopes that portion of the laterosensory canal segment or bearing a very limited bony flange along the anterior margin of the tube, but with the overall form of the bone nonetheless distinctly attenuated dorsally (Figure 18B). The dorsal tip of the fifth infraorbital in *Semaprochilodus* also falls distinctly short of the ventral margin of the sixth infraorbital, a separation at variance with the proximity of these bones in other prochilodontids and in proximate outgroups to that family.

Although the separation of the fifth and sixth infraorbitals present in *Semaprochilodus* is derived (based upon the association of these bones in some of the proximate outgroups, e.g., Chilodontidae, Vari et al., 1995, fig. 1), there is a range of forms of the fifth infraorbital even in basal groups in the Curimatidae (see Vari, 1989a, fig. 35), the first outgroup to the Prochilodontidae. This variation renders it impossible to a priori polarize the different states of that component of the ossification within the Prochilodontidae, and the condition of the fifth infraorbital in the outgroup is coded as unknown. The form of the fifth infraorbital is optimized as derived in *Semaprochilodus* under the most parsimonious hypothesis of relationships (see "Phylogenetic Reconstruction").

CHARACTER 72. Form of dorsal portion of fifth infraorbital. State 0: ?; State 1: Dorsal portion of fifth infraorbital distinctly wider than bony tube enclosing laterosensory canal segment in that bone and with dorsal margin that extends to proximate of ventral margin of sixth infraorbital; State 2: Dorsal portion of fifth infraorbital formed either by only bony tube, or bony tube with limited lateral flanges and with dorsal limit that falls distinctly short of ventral margin of sixth infraorbital.

The laterosensory canal segment in the fifth infraorbital in proximate outgroups to the Prochilodontidae usually has the form of a single tube in the Curimatidae (e.g., *Psectrogaster, Potamorhina, Curimatella,* see Vari, 1989a, fig. 35a–c), Anostomidae (e.g., *Pseudanos trimaculatus,* see Winterbottom, 1980, fig. 30), and Chilodontidae. A straight canal segment in the fifth infraorbital also occurs in *Ichthyoelephas,* but the members of that genus have in addition a distinctive series of small openings along the posterior margin of the canal segment (Figure 18C).

Ichthyoelephas also is distinctive in having a horizontally aligned, shelf-like, bony extension that arises from the dorsal portion of the main canal on the lateral surface of the fifth infraorbital. This bony process forms the ventral wall of a partially ossified laterosensory canal segment that extends posteriorly from the primary canal system in the fifth infraorbital to the rear of the adipose eyelid (Figure 18C) (structure present in all cleared and stained *Ichthyoelephas* specimens larger than 100 mm SL). Both the series of small apertures along the posterior margin of the main canal segment and the partial envelopment of the incompletely ossified canal on the anterior of the fifth infraorbital are absent in other prochilodontid genera and examined outgroups; thus, they are hypothesized herein to be derived features synapomorphic for the species of *Ichthyoelephas.*

CHARACTER 73. Lateral surface and main laterosensory canal segment in fifth infraorbital. State 0: Without series of small apertures along posterior margin of main laterosensory canal segment and without horizontal bony shelf that forms base of posteriorly directed laterosensory canal; State 1: With series of small apertures along posterior margin of main laterosensory canal segment and with bony shelf that forms base of posteriorly directed laterosensory canal.

Sixth Infraorbital

The laterosensory canal segment in the sixth infraorbital of the Prochilodontidae demonstrates phylogenetically useful intrafamilial variation at several levels. Within the first outgroup, the Curimatidae, the sixth infraorbital in basal lineages in the family (e.g., *Curimata, Psectrogaster,* see Vari, 1989a, fig. 36; with modifications in *Potamorhina*) has a tripartite laterosensory canal system. The ventral arm of the canal system contacts the laterosensory canal segment in the fifth infraorbital, the opening of the posterodorsal branch approximates the anterior opening of the pterotic sensory canal, and the anterodorsal branch contacts the sensory canal that extends through the frontal. This pattern of canal segments in the sixth infraorbital also is present in basal lineages of the Characiformes (Distichodontidae: *Xenocharax,* Daget, 1960, fig. 7; Citharinidae: *Citharidium,* Daget, 1962a, fig. 10; *Citharinus,* Daget, 1962b, fig. 7) and in the secondary outgroup to the Prochilodontidae in the Chilodontidae and the more generalized non-anostomine members of the Anostomidae (e.g., *Leporinus, Schizodon*). Such a tripartite pattern of the laterosensory canal segment in the sixth infraorbital is hypothesized to be plesiomorphic for the Prochilodontidae.

Two divergent modifications of this basic tripartite system in the sixth infraorbital occur within the Prochilodontidae. One occurs among all species of *Ichthyoelephas.* Although they retain the primary tripartite laterosensory canal in this bone, the basic pattern is supplemented by a series of relatively small, ramifying canals that exit from the main canal segment along the ventral two-thirds of its length (Figure 18C). This elaboration is unique to this genus among prochilodontids and proximate outgroups and is herein considered to be derived.

CHARACTER 74. Ramifying canals exiting from ventral two-thirds of main laterosensory canal segment in sixth infraorbital. State 0: Absent; State 1: Present.

A second modification occurs among the *Prochilodus* species. They have one, or more typically two, additional well-developed branches that extend anteriorly and posteriorly from the lateral margins of the main portion of the laterosensory canal in the sixth infraorbital (Figure 18A; note: number of canals intraspecifically variable in some species). Within proximate outgroups, the only elaborations of the sensory canal segment somewhat comparable to those present in *Prochilodus* occur in the species of *Potamorhina* in the Curimatidae (see Vari, 1984, fig. 3b; Vari, 1989a, fig. 36c). The morphology of the secondary canals in the sixth infraorbital of the Prochilodontidae and *Potamorhina* differ in various details (compare Figure 18A herein with Vari, 1989a, fig. 36c). Furthermore, given the numerous synapomorphies that define both the Curimatidae and the clades that include *Potamorhina* (Vari, 1989a:52 and 55, respectively) and the synapomorphies for the Prochilodontidae enumerated below, these elaborations of the laterosensory canal segments in the two genera are most parsimoniously considered to be homoplastic. The elaboration of the primitively tripartite canal system in the sixth infraorbital of *Prochilodus* is consequently considered to be a synapomorphy for the species of that genus.

CHARACTER 75. One or two additional well-developed branches that extend anteriorly and posteriorly from main laterosensory canal segment in sixth infraorbital. State 0: Absent; State 1: Present.

SUPRAORBITAL

In all species of the Prochilodontidae, the supraorbital, an ossification situated dorsal to the orbit, has an anterior process that extends anteriorly from the main body of the bone over the lateral margin of the lateral ethmoid to the posterior margin of the nares. The anterior limit of this portion of the supraorbital forms part of the nearly continuous series of ossifications around the nares. Two morphologies of the supraorbital occur within the Prochilodontidae. The anterior portion of the bone in *Ichthyoelephas* and *Prochilodus* continues the relatively flat plane of the main portion of the ossification. In *Semaprochilo-*

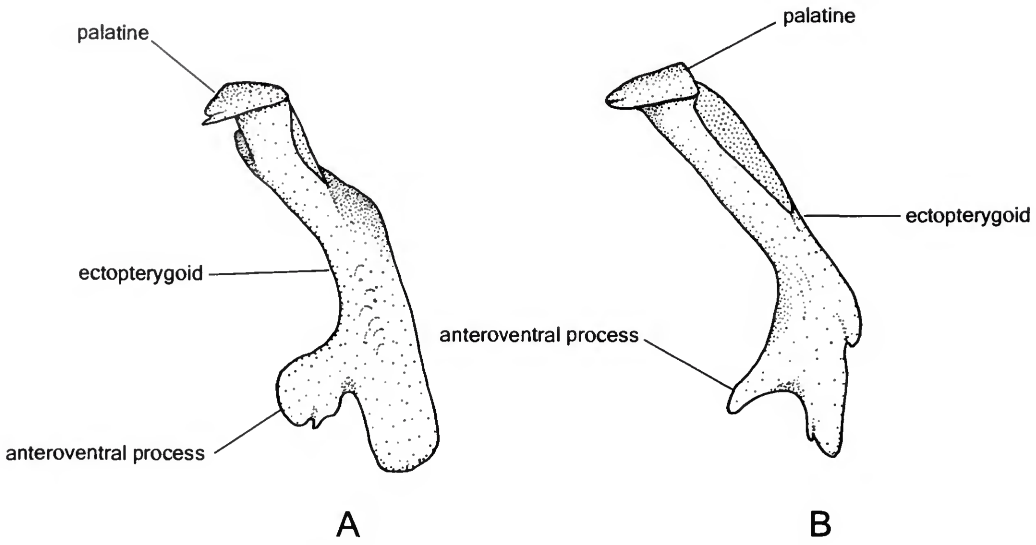


FIGURE 19.—Form of ectopterygoid: A, *Prochilodus vimboides*, USNM 345752; B, *Semaprochilodus brama*, MZUSP 21254; left side, lateral view, anterior to left. (Dense patterned stippling represents cartilage.)

dus, in contrast, the anterior portion of the supraorbital is more horizontally oriented than the remainder of the bone, with a distinct longitudinal fold present between the plane of the anterior margin of the supraorbital and the plane of the main portion of the bone. In light of its absence in proximate outgroups, this distinct longitudinal fold in the supraorbital in *Semaprochilodus* is considered to be derived.

CHARACTER 76. Orientation of anterior portion of supraorbital relative to remainder of bone. State 0: In same plane as main portion of bone; State 1: Anterior portion of bone more horizontally oriented than remainder of bone, with distinct fold between the two regions.

SUSPENSORIUM

The highly evertable jaws of the Prochilodontidae represent a major departure from the form of mobility of that system typical within the Characiformes. As would be expected, given the functional linkage of the jaws and the suspensorium, members of the Prochilodontidae demonstrate a series of modifications of the suspensorium correlated with eversion of the jaws. The restructurings of the various components of the suspensorium are discussed in terms of each bone in that complex.

Palatine

The palatine in the Prochilodontidae differs from the typical palatine of other groups within the Characiforms with respect to details of its association with the neurocranium and upper jaw and in its overall morphology. In the proximate outgroups to the Prochilodontidae, the families Curimatidae, Anostomidae, and Chilodontidae, the palatine demonstrates limited, if any, anterior-posterior mobility relative to the proximate ventral portions of the neurocranium. In the Prochilodontidae, in contrast, the entire suspensorium is characterized by pronounced internal mobility primarily along a parasagittal plane. Contributing to this system is the anterior-posterior motion of the palatine relative to the ventral portions of the neurocranium, with the mobility constrained by the suspensory system of connective tissue bands that connect the ventral surface of the neurocranium and the ectopterygoid and mesopterygoid.

The dorsal portion of the palatine in the Prochilodontidae abuts against the mesethmoid and is somewhat mobile, primarily in an anterior-posterior direction. The flattened ventral region of the mesethmoid in the area of contact is matched by a dorsally flattened palatine (Figures 8, 19) that has a pointed anterior process. No comparable morphology of the palatine was encountered elsewhere among examined characiforms. The mobility of the palatine with respect to the neurocranium together with the form of the ossification are considered to be derived within the Characiformes and are synapomorphic for the species of the Prochilodontidae.

CHARACTER 77. Form of palatine and its mobility relative to mesethmoid. State 0: Form not as in State 1 and with limited and no anteroposterior mobility of palatine relative to mesethmoid; State 1: Palatine dorsally flattened with pointed anterior process and with distinct anteroposterior mobility of palatine relative to mesethmoid.

The species of *Ichthyoelephas* differ from the remaining species in the family and proximate outgroups in having a distinct medial process on the ventral portion of the palatine. No such process has been found in examined outgroup characiforms, and its possession is hypothesized to be a synapomorphy for the members of the genus.

CHARACTER 78. Medial process on ventral portion of palatine. State 0: Absent; State 1: Present.

Ectopterygoid

As discussed by Vari (1983:30), members of the Prochilodontidae have a distinct form of ectopterygoid with a well-developed anteroventral process that results in an overall tripartite form to the bone (Figure 19, see also Vari, 1983, fig. 28). That morphology of the ectopterygoid contrasts with the anteriorly unelaborated form of that ossification typically present both in proximate outgroups to that family (e.g., Curimatidae, *Potamorhina latior,* Vari, 1983, fig. 27) and characiforms in general (e.g., *Brycon meeki,* Weitzman, 1962, fig. 10). Vari (1983) proposed that such a form of the ectopterygoid was a synapomorphy for the species of the Prochilodontidae, based upon an examination of a subset of species in that family. More encompassing surveys in this study have shown that a tripartite ectopterygoid is present in all prochilodontid species, and outgroup comparisons failed to reveal any other taxa with a similarly restructured ectopterygoid.

CHARACTER 79. Form of anterior portion of ectopterygoid. State 0: Without anterior process and not having overall tripartite form; State 1: With anterior process and having overall tripartite form.

The anteroventral process of the ectopterygoid is broadly rounded distally in all species of *Prochilodus* (Figure 19A) and *Ichthyoelephas* (Vari, 1983, fig. 28). *Semaprochilodus* species, however, have a varyingly falcate form of the anteroventral process of the ectopterygoid (Figure 19B). The lack of an anteroventral process of the ectopterygoid in outgroup characiforms renders it impossible to a priori polarize this intrafamilial variation in the shape of that process, and the condition in the outgroup is consequently scored as unknown. Under the most parsimonious hypothesis of relationships arrived at in this study, the falcate form of the structure in *Semaprochilodus* is optimized as derived (see "Phylogenetic Reconstruction," below).

CHARACTER 80. Form of distal portion of anteroventral process of ectopterygoid. State 0: Absent; State 1: Rounded; State 2: Varyingly falcate.

A second noteworthy aspect of the ectopterygoid in the Prochilodontidae previously noted by Vari (1983:30) is the pronounced degree of mobility of that bone relative to the quadrate. The occurrence of such mobility has been found herein to be general to all members of that family; however, mobility between the ectopterygoid and quadrate is not unique to the Prochilodontidae in the Characiformes, as it is also characteristic of the Hemiodontidae and Parodontidae. As noted by Vari (1983:30), the ectopterygoid-quadrate mobility in the Hemiodontidae and Parodontidae results from a series of modifications that are different than those that permit intra-suspensorium mobility in the Prochilodontidae. Furthermore, the Hemiodontidae and Parodontidae are more closely related to groups other than the Prochilodontidae within the Characiformes, as indicated both by the results of this and prior studies (Vari, 1983; Buckup, 1998). The mobility of the ectopterygoid relative to the quadrate in the Prochilodontidae is consequently considered to be synapomorphic for the members of that family.

CHARACTER 81. Mobility between ectopterygoid and quadrate. State 0: Limited or no mobility between ectopterygoid and quadrate; State 1: Pronounced degree of mobility between ectopterygoid and quadrate.

Quadrate

One of the most distinctive attributes of the quadrate in the Prochilodontidae is its vertical mobility relative to the preopercle. Mobility between these two elements contrasts with the typical tight and immobile joint between the quadrate and preopercle in other characiforms. The vertical mobility of the quadrate on the preopercle is made possible by a number of modifications that include the deeply indented posterior margin of the quadrate (see Vari, 1983, fig. 28, for condition in *Ichthyoelephas*). As a consequence, the posterior portions of the quadrate extend a considerable distance along the lateral and medial margins of the anterior portion of the preopercle. The restructurings associated with this quadrate-preopercle mobility were discussed by Vari (1983:30) and were based upon a subset of prochilodontids; the reader is referred to that publication for a more detailed discussion. Analysis herein has demonstrated that such mobility occurs in all species in the Prochilodontidae, and based upon the outgroups examined in this study, we concur with Vari (1983) in considering the posteriorly deeply notched quadrate and the vertical mobility of that element with respect to the preopercle to be derived.

CHARACTER 82. Form of posterior portion of quadrate and vertical mobility of quadrate relative to preopercle. State 0: Posterior portion of quadrate without deep horizontal notch and with quadrate immobile relative to preopercle; State 1: Posterior portion of quadrate with deep horizontal notch and with quadrate distinctly mobile vertically relative to preopercle.

Several aspects of the quadrate also are phylogenetically informative at intrafamilial phylogenetic levels in the Prochilodontidae. The lateral shelf-like process along the ventral margin of the quadrate is more highly developed throughout the Prochilodontidae than it is in most taxa in the Characiformes (see comments in Vari, 1983:30–31). The lateral margin of the shelf-like process of the quadrate lies approximately at the vertical plane through the lateral margin of the articular facet of the quadrate in *Prochilodus* and *Semaprochilodus*. In *Ichthyoelephas,* the shelf-like process of the quadrate extends distinctly lateral of the articular facet of the quadrate, thereby providing an increased area of attachment for the enlarged adductor mandibulae muscles associated with the highly restructured jaws and expanded lips that are characteristic of that genus. This expansion of the shelf-like process along the ventral margin of the quadrate beyond the condition in *Prochilodus, Semaprochilodus,* and outgroups is hypothesized to be a synapomorphy for the species of *Ichthyoelephas*.

CHARACTER 83. Degree of development of lateral shelf-like process along ventral margin of quadrate. State 0: Shelf absent or poorly developed and falls short of parasagittal plane through lateral margin of articular facet of quadrate; State 1: Shelf extends laterally to vertical plane through lateral margin of articular facet of quadrate; State 2: Shelf extends distinctly lateral to vertical plane through lateral margin of articular facet of quadrate.

Turning to the medial surface of the quadrate, we find that the posterior portion of the quadrate extends medial of the preopercle as a relatively straight, approximately horizontally aligned structure in both *Prochilodus* and *Semaprochilodus*. The dorsal margin of that portion of the quadrate and the ventral border of the symplectic jointly delimit a distinct, albeit still acute, angle. Such an alignment corresponds to the orientation of the ventral portion of the quadrate that is present in numerous groups within the Characiformes, including proximate outgroups to the Prochilodontidae, and it is consequently considered to be the plesiomorphic condition. *Ichthyoelephas,* in contrast, has this posteromedial process of the quadrate distinctly more posterodorsally oriented, and as a consequence, the dorsal margin of the process approximates the ventral border of the symplectic. This reorientation eliminates the distinct angle between the margins of the two structures, whereas the angle is present in outgroups. The posterodorsal reorientation of the posteromedial process of the quadrate in *Ichthyoelephas* is, thus, considered to be derived and synapomorphic for the species of that genus.

CHARACTER 84. Orientation of posterior portion of quadrate medial of preopercle. State 0: Horizontally aligned and separated from symplectic; State 1: Posterodorsally aligned and in contact with symplectic.

Mesopterygoid

Within the Characiformes the mesopterygoid is nearly invariably closely united to the palatine and/or the ectopterygoid, or it is closely united to the cartilage body on the dorsal portions of the suspensorium that is varyingly enveloped by those two ossifications. This tight association between these elements renders motion between the mesopterygoid and the more anterior components of the suspensorium impossible in most characiforms. All species of the Prochilodontidae, in contrast, demonstrate a pronounced degree of mobility between the proportionally small mesopterygoid (see below) and the medial surface of the dorsoventrally elongate ectopterygoid (see Vari, 1983, fig. 28, for illustration of these bones). These modifications contribute to the pronounced overall intra-suspensorium mobility characteristic of the Prochilodontidae. Such a mode of achieving mesopterygoid-ectopterygoid mobility has not been encountered in examined outgroups within the Characiformes, and it is hypothesized to be synapomorphic for the Prochilodontidae.

CHARACTER 85. Mobility between mesopterygoid and ectopterygoid. State 0: Absent; State 1: Pronounced.

All species of *Prochilodus* and *Semaprochilodus* along with the members of the first outgroup to the Prochilodontidae, the Curimatidae, have a mesopterygoid that is approximately the same size, or only slightly smaller than, the metapterygoid. The species of *Ichthyoelephas,* in contrast, have a mesopterygoid that is significantly smaller than the metapterygoid (Vari, 1983, fig. 28), a condition hypothesized to be derived on the basis of the relative sizes of these ossifications in outgroups.

CHARACTER 86. Size of mesopterygoid. State 0: Approximately same size as metapterygoid; State 1: Distinctly smaller than metapterygoid.

Both *Ichthyoelephas* and *Semaprochilodus* have a relatively straight dorsal margin on the mesopterygoid, a condition that approximates the morphology of the bone in outgroups to the Prochilodontidae (e.g., Curimatidae, Vari, 1989a, fig. 41). Species of *Prochilodus* alternatively have the posterodorsal portion of the mesopterygoid proportionally reduced. This reshaping is reflected in the distinctly posteroventrally inclined posterodorsal region of the bone that, along with modifications of the metapterygoid, contributes to the distinct, acutely angled to variably rounded notch along the dorsal margin of the suspensorium (Figure 20). In light of its absence in outgroups, this reduction of the posterodorsal portion of the mesopterygoid in the species of *Prochilodus* is hypothesized to be derived.

CHARACTER 87. Dorsal margin of posterior portion of mesopterygoid. State 0: Relatively straight; State 1: Distinctly posteroventrally inclined.

Metapterygoid

The dorsal portion of the metapterygoid in the region where that ossification articulates with the mesopterygoid is typically unelaborated and has an approximately straight margin both in the Curimatidae (Vari, 1989a, fig. 41) and in the clade formed of the Anostomidae (Winterbottom, 1980, fig. 35) plus Chilodontidae (Vari et al., 1995, fig. 4), the sequential proximate outgroups to the Prochilodontidae. All genera of the Prochilodontidae have a more elaborate anterodorsal portion of the metapterygoid that is composed of two components (Figure 20). The first of these units is a lateral ridge that extends anteroventrally to the anterior margin of the bone and that continues onto the lateral surface of the mesopterygoid. The second component is a medial flange that contacts the posterior margin of the mesopterygoid. These modifications of the metapterygoid are unique to the Prochilodontidae among examined outgroups and consequently are considered to be derived.

CHARACTER 88. Dorsal portion of metapterygoid proximate to articulation with mesopterygoid. State 0: Unelaborated;

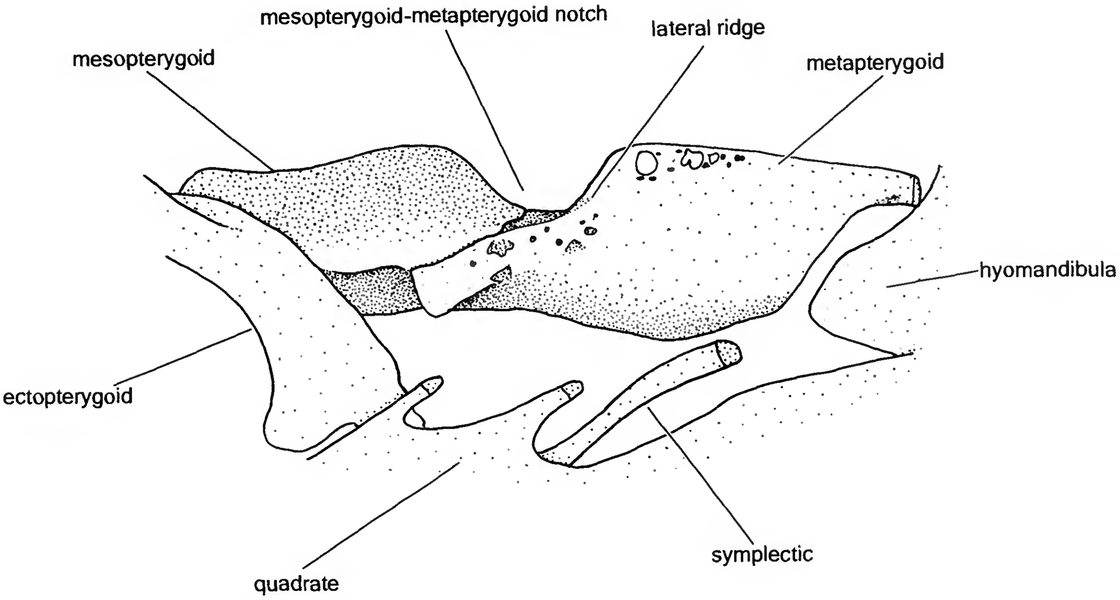


FIGURE 20.—Mesopterygoid and metapterygoid of *Prochilodus nigricans*, MZUSP 42682; left side, lateral view, anterior to left, proximate portions of neighboring elements of suspensorium outlined and lightly stippled.

State 1: Divided into two components; a lateral ridge and medial flange.

Prochilodus species are unique within the Prochilodontidae and among proximate outgroups to that family in having a reduction of the anterodorsal portion of the metapterygoid and a consequent anteroventrally angled anterior margin to the metapterygoid in the region proximate to the mesopterygoid-metapterygoid junction (Figure 20). In light of its absence in outgroups to the genus, this restructuring of that portion of the metapterygoid is considered to be derived for the species of *Prochilodus*. The cited reduction of the metapterygoid combined with the matching reduction of the posterodorsal margin of the mesopterygoid (see discussion under "Mesopterygoid," above) results is a pronounced concavity along the dorsal profile of the central section of the suspensorium (Figure 20).

This concavity along the margin of the suspensorium is positioned proximate to the medial margin of the blade-like lateral wing of the lateral ethmoid when the mouth is protracted. It seems likely that the concavity formed by the modifications of the mesopterygoid and metapterygoid in *Prochilodus* permits the anterior movement of the suspensorium during eversion of the jaws without interference from the lateral ethmoid.

CHARACTER 89. Anterodorsal margin of metapterygoid. State 0: Not reduced and relatively straight; State 1: Reduced and distinctly anteroventrally inclined.

The posterior portion of the metapterygoid also is restructured from the condition in outgroups, which have a relatively broad articular cartilage along the posterior margin of the ossification (e.g., *Potamorhina latior*, Vari, 1989a, fig. 27). In contrast, the posterior portion of the metapterygoid in the Prochilodontidae has a discrete, posteriorly directed, cartilage-capped process that is relatively narrow in *Prochilodus* (Figure 20) and *Semaprochilodus* and slightly wider in *Ichthyoelephas* (Vari, 1983, fig. 28). Regardless of the relative width of the process, this reduction in the extent of the articular cartilage along the posterior portion of the metapterygoid is hypothesized to be derived because of the absence of such modifications among other examined characiforms.

CHARACTER 90. Posterior portion of metapterygoid. State 0: With broad articular cartilage; State 1: With discrete, posteriorly directed, cartilage-capped process.

Symplectic

Both *Prochilodus* and *Semaprochilodus* have an elongate symplectic, with the anterior portion of the bone situated in a pocket on the medial surface of the quadrate. The posterior portion of the symplectic in these taxa, in turn, extends beyond the limits of the posteriorly and posterodorsally oriented processes on the posterior portion of the quadrate (Figure 20). In both of these genera, the posterior limit of the symplectic consequently is situated ventral of the region where the interhyal attaches to the medial surface of the preopercle. Such a proportionately elongate symplectic also is present in the first outgroup to the Prochilodontidae, the Curimatidae (e.g., *Potamorhina* and *Psectrogaster*, Vari, 1989a, fig. 41), and in other outgroup characiforms, and it is consequently considered to be the plesiomorphic condition within the Prochilodontidae. The species of *Ichthyoelephas* differ from the just-described generalized characiform condition in having a proportionally distinctly shorter symplectic that barely attains, or falls slightly short of, the rear of the posterodorsally oriented processes of the quadrate. The symplectic in *Ichthyoelephas* differs further by being distinctly separated longitudinally from the vertical through the area of attachment of the interhyal to the preopercle. These modifications are hypothesized to be derived, given their absence in outgroups.

CHARACTER 91: Posterior limit of symplectic. State 0: Reaches posteriorly distinctly beyond limits of posteriorly and posterodorsally oriented process on posterior portion of quadrate and is situated ventral of area of attachment of interhyal on preopercle; State 1: Barely attains, or falls short of, limits of posteriorly and posterodorsally oriented process on posterior portion of quadrate and is situated distinctly anterior of vertical through area of attachment of interhyal on preopercle.

Opercle

In his discussion of the opercle in a subset of characiforms, Vari (1983:29) reported that specimens of all sizes in examined species of the Curimatidae, along with juveniles and smaller individuals of the Prochilodontidae, all have a posteroventrally aligned, dorsally undercut flange situated on the anterodorsal portion of the opercle that presumably serves to strengthen the opercle in these detritivorous fishes. Such an opercular flange is retained throughout ontogeny in the Curimatidae (see Vari, 1983, fig. 27), but in the Prochilodontidae that discrete morphology of the flange is only readily apparent in juvenile specimens of approximately 20 to 30 mm SL. Towards the upper portion of this size range the flange develops a series of bony ridges that extend outwards at approximately right angles from the main axis of the flange. These secondary ridges progressively coalesce ontogenetically such that the flange in prochilodontids of moderate to large body sizes no longer forms a discrete lateral ridge, being instead restructured into a gently sloping, thickened area on the lateral surface of the opercle. This further elaboration of the flange was hypothesized to be unique to, and synapomorphic for, the members of the Prochilodontidae by Vari (1983:29) based upon an examination of a subset of the species in the family. That hypothesis is supported by the examination of a more extensive series of specimens in this study.

Although a distinct opercular flange also is present in the microphagous filter-feeders of the African characiform family Citharinidae, that process differs in overall morphology from the flange in juveniles of the Prochilodontidae and in specimens of all sizes in the Curimatidae. Above and beyond these morphological differences, the phylogenetic relationships of the Citharinidae lie with the Distichodontidae (Vari, 1979).

CHARACTER 92. Posteroventrally aligned flange on dorsolateral surface of opercle. State 0: Flange either absent throughout ontogeny or if present at any point in ontogeny then distinct even in adults; State 1: Distinct flange present in very small specimens progressively eliminated ontogenetically by development and coalescence of secondary flanges and replaced by thickened area on opercle.

Preopercle

Roberts (1973b:218, fig. 19) reported that the portion of the laterosensory canal system situated ventral of the quadrate in the Prochilodontidae is restructured into two independent tubular ossifications, which he termed the subpreopercular canal bones. The presence of tubular ossifications in that location in both the Prochilodontidae and the Anostomidae was proposed by Roberts as evidence of a close phylogenetic relationship of those families. Winterbottom (1980:37, figs. 35, 36, 39) alternatively considered the independent tubular ossifications ventral of the anterior portion of the quadrate in the Anostomidae to be components of an anteriorly subdivided preopercle. Vari (1983:31) questioned the homology of the independent subquadrate canal-bearing bones anterior to the main portion of the preopercle in the Prochilodontidae and Anostomidae as proposed by Roberts (1973b) on both phylogenetic and functional grounds. As a consequence, Vari (1983) recognized the presence of such separate bones that surround the laterosensory canal segment situated ventral of the quadrate as being a portion of the preopercle following Winterbottom's terminology. Vari (1983) also utilized the presence of such ossifications in a sample of members of the Prochilodontidae as a synapomorphy for that family. Our examination of cleared and stained specimens of all prochilodontids has confirmed that the presence of such ossifications is universal in the family.

Examination of a broader range of cleared and stained specimens of all species of the Prochilodontidae demonstrated that the number of separate tubular anterior preopercle elements is ontogenetically variable. The smallest examined cleared and stained specimens of prochilodontids (*P. mariae,* 18.5 mm SL; USNM 256959; *P. nigricans,* 12.8–13.6 mm BL, LIRP 1312) lack separate ossifications of the anterior portion of the preopercular laterosensory canal. The smallest examined prochilodontid with such ossifications apparent is a 26 mm SL specimen of *P. mariae,* and by 35 mm SL that species has four short, well-separated tubes in that region. These bones apparently coalesce ontogenetically with the former limits of the individual ossifications delimited by the ventrally directed pores present in the fused elements. Larger cleared and stained specimens of *P. mariae* (92.6–97.1 mm SL) have two separate ossifications, and the largest cleared and stained *Prochilodus* specimen examined (*P. britskii,* 192.6 mm SL, MZUSP 38856) has a only single tubular ossification ventral of the quadrate. In the case of *Ichthyoelephas,* cleared and stained specimens of *I. humeralis* of medium size (108.5–133.6 mm SL) have two independent tubular ossifications ventral of the quadrate, with the same number of separate elements present in the cleared and stained specimen of *I. longirostris* (311.2 mm SL), the largest prochilodontid prepared in that manner in this study. More encompassing studies of larger series of cleared and stained specimens of all species of the Prochilodontidae are necessary to determine whether all members of the family demonstrate a progressive reduction in the number of components of this portion of the preopercular laterosensory canal and whether the apparent generic-level variation in the number of ossifications in adult prochilodontids is phylogenetically informative.

CHARACTER 93: Anterior portion of preopercular laterosensory canal. State 0: Continuous anterior to region proximate to articular facet of quadrate; State 1: Subdivided, with anterior portion formed of one or more independent bony tubes situated between region of articular facet of quadrate and main body of preopercle.

Turning to the main body of the preopercle we find phylogenetically useful variation on both the lateral and medial surfaces of that ossification in the Prochilodontidae. In the species of *Prochilodus* and *Semaprochilodus*, the laterosensory canal segment in the preopercle has three or four simple secondary canals that extend posteriorly and posteroventrally from the angle of the ossification. In *Ichthyoelephas*, these secondary canals of the laterosensory canal segment are much more highly ramified than is the situation in either *Prochilodus* or *Semaprochilodus* or among proximate outgroups to the Prochilodontidae. The elaboration of these secondary canals is, thus, hypothesized to be a synapomorphy for the species of *Ichthyoelephas*.

CHARACTER 94: Laterosensory canal system in ventral portion of preopercle. State 0: With three or four simple or moderately developed but not ramified secondary canals at angle of ossification; State 1: With series of highly ramified secondary canals at angle of ossification.

The medial surface of the horizontal portion of the preopercle is typically unelaborated within the Characiformes, or it has at most a slight medial swelling or longitudinal ridge along the horizontal portion of the laterosensory canal segment in that bone. All prochilodontids instead have a distinct, horizontal, shelf-like process that begins ventral of the medial process of the quadrate and extends along the medial surface of the anterior portion of the preopercle. The shelf-like process extends for varying distances along the horizontal portion of the preopercle and is considered to be a synapomorphy for the family in light of its absence in examined outgroups.

CHARACTER 95. Medial surface of horizontal portion of preopercle. State 0: Unelaborated or with slightly developed, longitudinal ridge; State 1: With distinct, horizontal, shelf-like ridge.

In *Prochilodus* and *Semaprochilodus*, the horizontal medial ridge on the preopercle is moderately developed and almost horizontally aligned. *Ichthyoelephas* differs from other prochilodontids in having a proportionally more developed process with a more dorsomedial alignment of the ridge. These features are particularly developed in the single examined cleared and stained specimen of *I. longirostris*, which is distinctly larger than the available cleared and stained specimens of *I. humeralis*. In the absence of such a ridge in outgroups, it is impossible to a priori polarize the two forms of the process, and the condition in the outgroup is scored as unknown. The more highly developed and more dorsomedially aligned medial ridge on the preopercle in *Ichthyoelephas* is optimized as derived in the final most parsimonious hypothesis of relationships (see "Phylogenetic Reconstruction").

CHARACTER 96. Degree of development and alignment of medial ridge on the preopercle. State 0: Absent; State 1: Moderately developed and almost horizontally aligned; State 2: Highly developed and dorsomedially inclined.

Interopercle

The interopercle among examined characiforms is typically a primarily transversely flattened ossification without elaborations of its dorsal regions. Members of the Prochilodontidae, however, have the anterodorsal portion of the interopercle transversely widened into a distinct articular surface that conforms to the shape of the ventral surface of the shelf-like process present on the lateral surface of the anterior portion of the preopercle. In light of its absence in outgroups, the presence of this articular process on the interopercle in all members of the Prochilodontidae is considered to be derived.

CHARACTER 97. Transversely widened articular surface on anterodorsal portion of interopercle. State 0: Absent; State 1: Present.

The articular surface on the interopercle is comparatively moderately developed in all *Prochilodus* species and is particularly well developed in the species of *Ichthyoelephas* and *Semaprochilodus*. In the absence of an articular surface on the anterodorsal portion of the interopercle in outgroups, it is impossible to a priori polarize the two conditions of the articular surface, and the outgroup condition is coded as unknown. The more highly developed articular surface in *Ichthyoelephas* and *Semaprochilodus* is optimized as synapomorphic for that pair of genera within the final most parsimonious hypothesis of relationships (see "Phylogenetic Reconstruction").

CHARACTER 98. Degree of development of articular surface of anterodorsal portion of interopercle. State 0: Absent; State 1: Moderately developed; State 2: Highly developed.

Suprapreopercle

The suprapreopercle carries the laterosensory canal segment between the dorsal termination of the main body of the preopercle and the ventrolateral margin of the neurocranium. The suprapreopercle in the Characiformes is in the shape of a varyingly elongate tube that sometimes apparently fuses onto the preopercle (e.g., some members of the African family Alestidae). An unfused tubular suprapreopercle is the general condition throughout the Curimatidae, Anostomidae, and Chilodontidae, the proximate outgroups to the Prochilodontidae.

Within the Prochilodontidae, this ossification is present in all *Ichthyoelephas* and *Prochilodus* species and in the majority of species of *Semaprochilodus*, but it is absent in *S. insignis* and *S. kneri*. Given the general presence of the suprapreopercle in successive outgroups, its absence is hypothesized to be a derived loss that is synapomorphic for those two species.

CHARACTER 99. Suprapreopercle. State 0: Present; State 1: Absent.

CRANIUM

The neurocranium of the members of the Prochilodontidae demonstrates numerous restructurings relative to the conditions in proximate outgroups, and indeed to all characiforms. Many of these modifications in prochilodontids are apparently associated with the highly modified jaws that are characteristic of the family. In light of the extensive series of previously discussed derived characters that support the hypothesis of the monophyly of the family, our comparative studies of the neurocranium focus either on features that (1) define subgroups within the Prochilodontidae, (2) are directly associated functionally with complexes discussed in the preceding sections, or (3) have been previously discussed in the literature.

Mesethmoid

The dramatic restructuring of the upper-jaw bones detailed previously is reflected in modifications of the ventral portion of the mesethmoid of prochilodontids. Contrary to the condition in the Curimatidae, Anostomidae, and Chilodontidae, all members of the Prochilodontidae have a distinct, longitudinally elongate, laterally compressed, ventromedial process that extends between, and completely separates, the contralateral premaxillae (Figure 21). Although ventromedial processes of the mesethmoid also occur in some characid characiforms (e.g., *Creagrutus*, Vari and Harold, 2001:30, fig. 14; *Gymnocharacinus*, Miquelarena and Arámburu, 1983, fig. 3), those revampings of that portion of the mesethmoid differ in diverse details from the processes present in the Prochilodontidae. Furthermore, the outgroups with such modifications are, as members of the Characidae, phylogenetically distant from the Prochilodontidae. The occurrence of ventral medial expansions of the mesethmoid in the Prochilodontidae and in some taxa in the Characidae are consequently hypothesized to be homoplastic. In light of that situation, the presence of such a longitudinally elongate mesethmoid process is hypothesized to be a synapomorphy for the species of the Prochilodontidae.

CHARACTER 100. Ventral surface of mesethmoid. State 0: Unelaborated; State 1: With laterally compressed, ventromedial process.

Another notable feature of the mesethmoid among prochilodontids is the pronounced intrafamilial disparity in the relative size of the ossification. In both *Prochilodus* and *Semaprochilodus*, the anterior portion of the mesethmoid that is situated proximate to the medial portion of the contralateral premaxilla is moderately wide, with its width approximately the same as, or slightly wider than, that of the median frontal fontanel. Although this type of mesethmoid is wider than the condition of the bone present in proximate outgroups, the form of that portion of the mesethmoid in *Prochilodus* and *Semaprochilodus* most closely approximates the form in outgroups to the Prochilodontidae. In *Ichthyoelephas*, in contrast, that portion of the mesethmoid is proportionally notably larger, with a width that is distinctly more than twice that of the median frontal fontanel (see Roberts, 1973b, fig. 2, for condition in *Ichthyoelephas* and Miles, 1943, figure on page 46, for comparisons of the relative size of the mesethmoid (the dermethmoid of that author) in *Ichthyoelephas longirostris* and *Prochilodus magdalenae*).

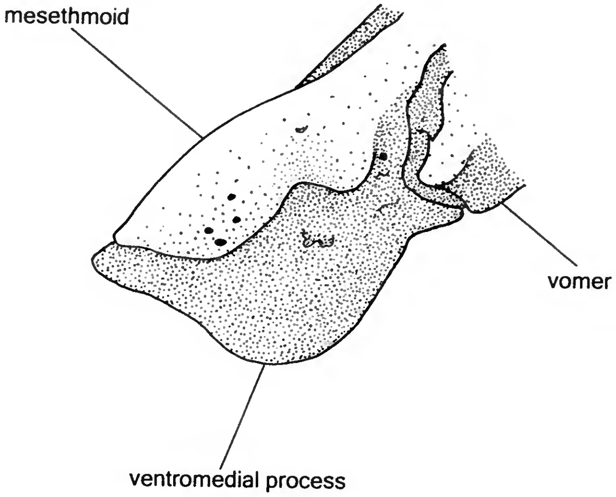


FIGURE 21.—Mesethmoid and anterior portion of vomer of *Prochilodus vimboides*, USNM 345742; left side, lateral view.

CHARACTER 101. Relative size of portion of mesethmoid that contacts medial portions of contralateral premaxillae. State 0: Anterior portion of mesethmoid only moderately wide; width approximately equal to width of frontal portion of median cranial fontanelle; State 1: Anterior portion of mesethmoid distinctly wide; width more than twice width of frontal portion of median cranial fontanelle.

Vomer

The anterior portion of the vomer that abuts against the ventral surface of the mesethmoid is relatively small in *Prochilodus* and *Semaprochilodus*, and basal curimatids (e.g., *Curimatopsis*) have a similar morphology. *Ichthyoelephas* species, in contrast, have that portion of the vomer expanded into a large, rounded structure that contacts both the medial surface of the anterior process of the lateral ethmoid and the anteromedial portion of the main body of that ossification (see Roberts, 1973b, fig. 4). In light of the unique nature of such an enlargement of the vomer in *Ichthyoelephas* within the Prochilodontidae and given the condition in basal units of proximate outgroups, the morphology of the bone in that genus is considered to be derived.

CHARACTER 102. Form of anterior portion of vomer. State 0: Not as in State 1; State 1: In form of large, horizontally rounded structure that contacts anterior process and main body of lateral ethmoid.

Lateral Ethmoid

The anterior face of the lateral ethmoid of all prochilodontids has a relatively narrow (*Prochilodus*) to moderately wide (*Ichthyoelephas* (Roberts, 1973b, fig. 4) and *Semaprochilodus*) process that extends forward from the anterior surface of the bone to contact the lateral keel-like process on the ventrolateral surface of the mesethmoid (see also Roberts, 1973b:216). Among proximate outgroups to the Prochilodontidae, the process is either absent in toto in many members of the Curimatidae or is limited to a narrow process that extends anteriorly to contact the lateral surface of the widened vomer in the largest examined cleared and stained specimens of the Curimatidae. As a consequence, the Curimatidae lacks contact between the lateral ethmoid and the mesethmoid. In the clade formed of the Anostomidae and Chilodontidae, the second outgroup to the Prochilodontidae, the anterior process of the lateral ethmoid is narrow, more so in the Anostomidae, and extends forward to the mesethmoid in the Anostomidae and to the vomer in the Chilodontidae. A narrow anterior process of the lateral ethmoid that contacts the vomer is similarly present in basal characiforms (e.g., *Xenocharax*). Given the information from the secondary outgroup and basal characiforms, it appears that a narrow form of the anterior process of the lateral ethmoid is plesiomorphic for the Prochilodontidae. Under that hypothesis the wider form of the anterior process of the lateral ethmoid in *Ichthyoelephas* and *Semaprochilodus* is synapomorphic for that pair of genera.

CHARACTER 103. Anterior process of lateral ethmoid. State 0: Narrow; State 1: Wide.

The pronounced reduction or loss of the anterior process of the lateral ethmoid in all examined members of the Curimatidae is another potential synapomorphy for the members of that family, given the presence of that process in proximate outgroups to that family. If that feature proves to be common to all members of the family, it would add to the nineteen synapomorphies for the Curimatidae proposed by Vari (1983:48; 1989a:52).

In his discussion of the Prochilodontidae, Roberts (1973b: 216) reported that the blade-like lateral portions of the lateral ethmoid (the orbital blade or lamina of his terminology) "were highly fenestrated." Fenestration of that portion of the lateral ethmoid in prochilodontids demonstrates several discrete patterns. In *Ichthyoelephas,* the fenestration involves much of the blade-like portion of the bone (see Roberts, 1973b, fig. 4), and a similar distribution, although not of comparable density, of these openings also occurs in *Semaprochilodus.* In *Prochilodus,* the fenestration is restricted to the ventral border of the ossification and often is restricted to a distinct band proximate to the ventral margin of the bone. The presence of such distinct fenestration is unique to the Prochilodontidae among examined characiforms, including basal groups in the order; consequently, it is hypothesized to be derived. In light of the absence of such fenestration of the lateral ethmoid in other characiform groups, it is impossible to polarize the various arrangements and relative size of the fenestrae, and only the presence versus absence of the fenestrae are coded herein.

CHARACTER 104. Pronounced fenestration of at least a portion of blade-like lateral portions of lateral ethmoid. State 0: Absent; State 1: Present.

Orbitosphenoid

The association between the orbitosphenoid and the parasphenoid demonstrates a notable amount of variation across the characiforms. Basal characiforms (e.g., *Xenocharax,* Daget, 1960, fig. 8; *Citharinus,* Daget, 1962, fig. 6) have a broad area of contact between the ventral portion of the orbitosphenoid and the dorsal surface of the parasphenoid. Within more derived groups of characiforms such contact between these bones often is absent (e.g., *Brycon,* Weitzman, 1962, fig. 3), although it often is present in groups with dorsoventrally compressed skulls (e.g, *Ctenolucius,* Roberts, 1969, fig. 15) in which the compression brings the main bodies of the orbitosphenoid and parasphenoid into apparently secondary contact. Examination of the clade formed by the Curimatidae plus Prochilodontidae revealed that all species of the Curimatidae and the species of *Prochilodus* share a comparable form of contact between the orbitosphenoid and the parasphenoid (Figure 22A). In *Prochilodus,* the orbitosphenoid has an anteroposteriorly extensive ventromedial wing that contacts a slight dorsomedial ridge on the parasphenoid. This ventral process of the orbitosphenoid extends anteriorly to contact the anterolateral process of the orbitosphenoid that, in turn, contacts the posterior of the lateral ethmoid. The curved posterior margin of the orbitosphenoid forms the anterior margin of a rotund median opening delimited by that bone, the parasphenoid, the prootic, and the pterosphenoid.

Semaprochilodus and *Ichthyoelephas* demonstrate a reduction and loss, respectively, of this ventral process of the orbitosphenoid. *Semaprochilodus* (Figure 22B) lacks the anterior portion of the ventral portion of the orbitosphenoid present in *Prochilodus* and the Curimatidae (see next paragraph with respect to condition in *Ichthyoelephas*). As a consequence of the loss of the anterior portion of the orbitosphenoid, the posteroventral component of that ossification in *Semaprochilodus* is reduced to a bar-like, slightly posteroventrally oriented process that extends ventrally from the main body of the ossification to

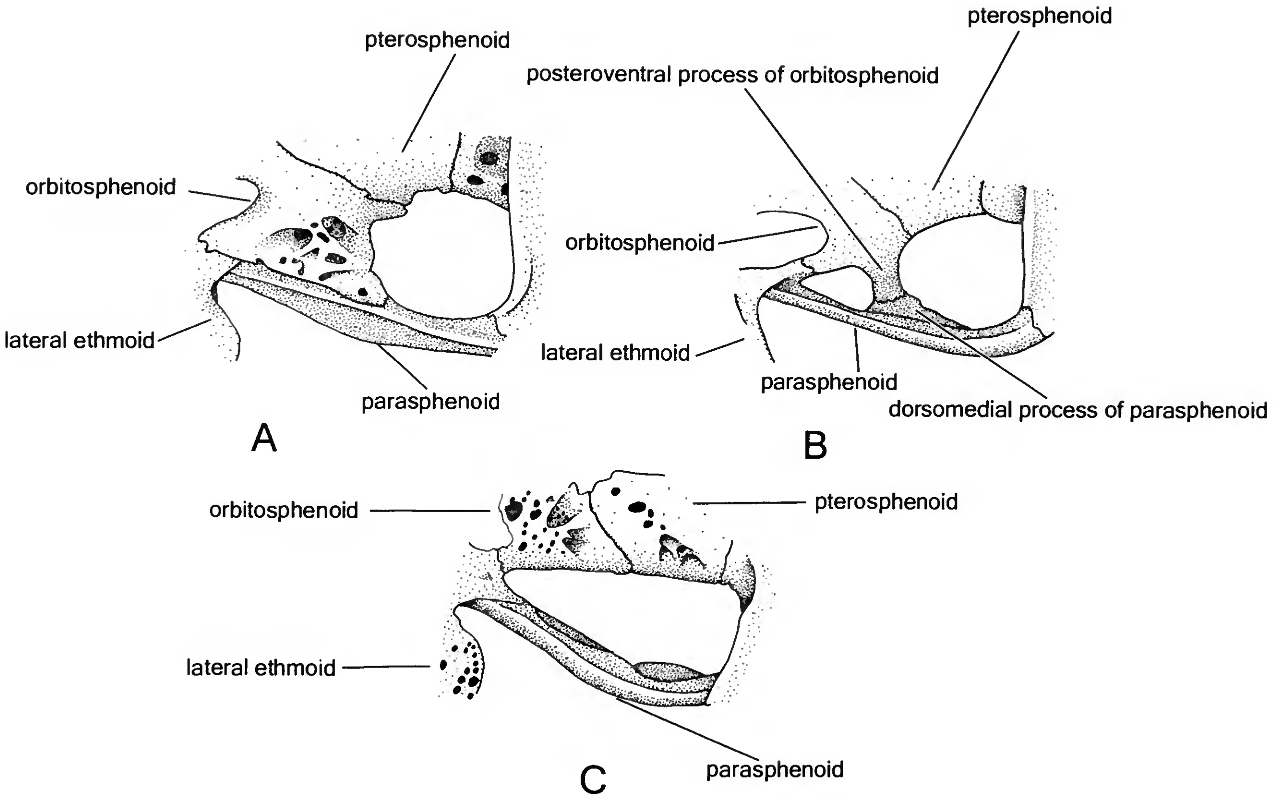


FIGURE 22.—Orbitosphenoid and proximate ossifications: A, *Prochilodus vimboides*, USNM 345752; B, *Semaprochilodus brama*, MZUSP 21254; C, *Ichthyoelephas humeralis*, USNM 231437; left side, lateral view, anterior to left; drawings not to scale.

contact the dorsomedial ridge on the parasphenoid. The ventrally reduced orbitosphenoid together with the parasphenoid and the lateral ethmoid encircle a median foramen in the neurocranium, with the posterior margin of the orbitosphenoid nonetheless retaining a form of that median aperture comparable with that in curimatids and *Prochilodus*. In *Ichthyoelephas*, the reduction of the orbitosphenoid is carried further, with a complete loss of the ventromedial process of the ossification (Figure 22C). As a consequence, the orbitosphenoid in *Ichthyoelephas* forms the dorsal, rather than the anterior, margin of the large central fenestra in the neurocranium and lacks any contact with the parasphenoid.

The forms of the orbitosphenoid in examined outgroups lead us to hypothesize that these progressive reductions of the orbitosphenoid are synapomorphies at two levels of inclusiveness. The loss of the anterior portion of the ventral process of the orbitosphenoid in the species of *Semaprochilodus* and *Ichthyoelephas* is considered to be derived for that pair of genera. The loss of the posterior section of that part of the bone is, in turn, considered to be a synapomorphy for the species of *Ichthyoelephas*.

CHARACTER 105. Extent of ventromedial process of orbitosphenoid. State 0: Anteroposteriorly extensive medial ventral wing extends anteriorly to anterolateral process of orbitosphenoid that contacts posterior of lateral ethmoid; State 1: Anterior portion of process in State 0 absent, and ventral process of orbitosphenoid limited to bar-like, posteroventrally oriented process; State 2: Ventral process of orbitosphenoid completely absent.

Parasphenoid

The dorsal surface of the parasphenoid is either unelaborated or has a slight dorsomedial ridge in proximate outgroups to the Prochilodontidae, a condition that also occurs in *Prochilodus* (Figure 22A) and *Ichthyoelephas* (Figure 22C). The species of *Semaprochilodus* (Figure 22B) have instead a proportionally significantly larger, anterodorsally elongate, dorsomedial ridge that begins under, and is highest at, the bar-like posteroventral portion of the orbitosphenoid that is present in the members of that genus. Posterior of the area of contact, the dorsomedial ridge gradually becomes shallower and terminates posteriorly in the region where the lateral processes of the parasphenoid extend dorsally to contact the prootic. In light of the absence of such a well-developed dorsomedial ridge on the parasphenoid of other prochilodontids or among the members of proximate outgroups, we consider the possession of such a structure on the parasphenoid to be a synapomorphy for the species of *Semaprochilodus*.

CHARACTER 106. Dorsomedial ridge along parasphenoid. State 0: Absent or slightly developed; State 1: Highly developed.

Frontal

The frontals in most characiforms are completely separated middorsally by the well-developed, fronto-parietal fontanel, with the contact between the contralateral frontals being limited to the transversely aligned epiphyseal bar. That condition also is present in *Prochilodus* and *Semaprochilodus*. The species of *Ichthyoelephas* instead have the posterior portions of the contralateral frontals in broad contact medially (Roberts, 1973b, fig. 2). A separation of the medial margins of the posterior portions of the frontals by a distinct fronto-parietal fontanel is universal in the Curimatidae, the first outgroup to the Prochilodontidae, even among species that have the anterior portion of the opening reduced (see Vari, 1991, fig. 10). Within the Chilodontidae and Anostomidae, the families that jointly form the second outgroup to the Prochilodontidae, we find a comparable, wide separation of the parietals in both genera in the Chilodontidae (*Caenotropus* and *Chilodus*) and in most of the apparently more basal examined genera in the Anostomidae (*Leporellus, Leporinus, Schizodon, Rhytiodus*). An almost complete closure of the entire fontanel occurs in the non-anostomine anostomid genus *Abramites*, and medial contact of the posterior portions of the frontals is universal in anostomine anostomids (see Winterbottom, 1980, fig. 53). Members of the Anostomidae with a reduction in the degree of separation of the frontals form a derived lineage, and a complete separation of the contralateral frontals appears to be plesiomorphic within that family. Because of the complete separation of the frontals in all, or at least basal components of, successive outgroups to the Prochilodontidae, we consider the closure of the posterior portion of the frontal region of the fontanel in *Ichthyoelephas* to be derived, albeit homoplastic to the apparently similar condition present in *Abramites* and the subfamily Anostominae of the Anostomidae, a component of the secondary outgroup to the Prochilodontidae.

CHARACTER 107. Median contact of posterior portions of contralateral frontals. State 0: Absent; State 1: Present.

Parietal

The medial margins of the contralateral parietals are separated by the well-developed, fronto-parietal fontanel in the first outgroup to the Prochilodontidae, the Curimatidae (see Vari, 1991, fig. 10). The second outgroup, the clade that consists of the Chilodontidae and Anostomidae, has a comparable, wide separation of the parietals in both genera of the Chilodontidae (*Caenotropus* and *Chilodus*). A distinct separation of the parietals also occurs in apparently basal genera of the Anostomidae (*Leporellus, Leporinus, Schizodon, Rhytiodus*). A reduction in the degree of separation of the parietals occurs in the subfamily Anostominae of the Anostomidae (see Winterbottom, 1980, fig. 53), with limited contact of the anterior portions of the parietals in large specimens of members of that subfamily (Winterbottom, 1980:41). Other than the Anostominae, the only member of the Anostomidae with a reduction in the extent of the fontanel is the monotypic genus *Abramites*, which has an area of broad contact between the anterior portions of the parietals. Members of the Anostomidae with a reduction in the degree of separation of the parietals are highly modified in numerous features, and the distinct medial separation of the bones appears to be plesiomorphic within that family. Thus, separation of the parietals is general, at least in basal components, to all proximate outgroups to the Prochilodontidae.

Completely separated parietals occur in all examined cleared and stained specimens of *Prochilodus* (largest specimen 192.6 mm SL) and *Semaprochilodus* (largest specimen 114.8 mm SL), whereas *Ichthyoelephas humeralis* specimens of sizes comparable to, or smaller than (108.5–133.6 mm SL), those of examined specimens of *Prochilodus* and *Semaprochilodus* have the parietals in contact along their entire medial margins (see also Roberts, 1973b, fig. 2). A comparable contact of the contralateral parietals also occurs in the single, significantly larger (311.2 mm SL) cleared and stained specimen of *I. longirostris* examined in this study, albeit with a decrease in the relative extent of the area of contact between the bones as a consequence of the relatively anteroposteriorly narrow parietals that are characteristic of the species (see also comments on the parietal, below). Roberts (1973b:216) reported that in "large adults of the Prochilodontidae frontoparietal fontanel sometimes entirely closed," but he did not provide a source for that statement. The "study material" cited by Roberts is of body sizes comparable to the cleared and stained material examined in this study, all of which retain distinct openings of the fontanel. The absence of appropriate skeletal preparations makes it impossible to determine the extent of the fontanel in very large specimens of *Prochilodus* and *Semaprochilodus*. Nonetheless, the large-sized whole specimens of both genera examined in this study demonstrate an open fontanel in the same region where the contralateral parietals are in contact in *Ichthyoelephas* species. In light of the separation of the parietals throughout ontogeny in the first outgroup to the Prochilodontidae and in all but a derived component of one clade in the second outgroup to that family (subfamily Anostominae of the Anostomidae), the broad medial contact of the parietals in both *Ichthyoelephas* species is considered to be derived.

CHARACTER 108. Contact of contralateral parietals along dorsal midline. State 0: Absent; State 1: Present.

Examined specimens of *Ichthyoelephas humeralis* (108.5–133.6 mm SL) have parietals that contribute to a significant portion of the posterodorsal surface of the cranium (see Roberts, 1973b, fig. 2). Such a morphology of the parietals is universal within *Prochilodus* and *Semaprochilodus* and is present in all examined members of proximate outgroups to the Prochilodontidae. In the single cleared and stained specimen of *I. longirostris* (311.2 mm SL), the dorsally exposed portion of the parietal is significantly reduced, being limited for its lateral two-thirds to a very narrow strip that carries the supratemporal canal of the laterosensory system along the posterior border of the parietal. This reduction of the exposed portion of the parietal in *I. longirostris* is unique to this species, both in the Prochilodontidae and among proximate outgroups and is, thus, considered to be derived. As an autapomorphy for the species, it is not included in the data matrix.

In his illustration of the neurocranium of *I. longirostris*, Miles (1943:46, unnumbered figure) illustrated the parietal as being positioned entirely along the posterior margin of the skull. That detail of the illustration provided by Miles is at variance with the condition of the parietal present in our examined cleared and stained specimen of that species in which that ossification contributes slightly to the dorsal portion of the neurocranium.

In both *Ichthyoelephas* (see Roberts, 1973b, fig. 2) and *Prochilodus*, the medial portion of the border between the frontal and parietal either extends almost directly transversely or has a moderately anteriorly directed alignment. Alignments similar to these occur in proximate outgroups to the Prochilodontidae (see Vari, 1991, fig. 10 for Curimatidae; Winterbottom, 1980, figs. 53, 56 for Anostomidae). The species of *Semaprochilodus* instead have an overall sigmoid contact dorsally between these bones, with the lateral portion of the border aligned somewhat anteromedially and the medial portion aligned posteromedially. The posterior orientation of the medial portion of the border is more pronounced in large cleared and stained individuals of *Semaprochilodus*, which apparently is a consequence of the ontogenetic extension of the posterior portion of the frontal over the anterodorsal surface of the parietal. Given the absence of such an alignment of the medial portion of the border between the frontal and parietal in proximate outgroups to the Prochilodontidae, that form of the border between these bones is considered to be a synapomorphy for the species of *Semaprochilodus*.

CHARACTER 109. Alignment of border between frontal and parietal on dorsal surface of cranium. State 0: Border aligned nearly directly transversely or with moderate anteromedial alignment; State 1: Medial portion of border posteromedially aligned, more so in large individuals.

Sphenotic

The sphenotic in proximate outgroups to the Prochilodontidae typically lacks a distinct fenestra that passes between the anterior surface of the bone that delimits the posterodorsal portion of the orbital cavity and the posterior surface of the ossification that forms the anterior section of the dilatator fossa. All prochilodontids instead have a distinct passage through the bone that either has the form of a single distinct aperture in *Prochilodus* and *Semaprochilodus* or consists of several closely conjoined openings in *Ichthyoelephas*. A comparable passage through the main portion of the sphenotic among proximate outgroups to the Prochilodontidae occurs only in the Curimatidae where such an aperture is, however, present only in *Curimata inornata* among examined species. *Curimata* is deeply nested within the phylogeny of the Curimatidae (Vari, 1989a, fig. 44), and *C. inornata* is a highly derived member of that genus (Vari, 1989b, fig. 14). As a consequence, it is most parsimonious to hypothesize that the presence of the passage through the sphenotic in the Prochilodontidae is homoplastic relative to the occurrence of a similar aperture in *C. inornata*. The possession of a passage through the sphenotic is a synapomorphy for the species of the Prochilodontidae.

CHARACTER 110. Fenestra that extends between the anterior surface of sphenotic that borders orbital cavity and posterior surface of bone in dilatator fossa. State 0: Absent; State 1: Present.

Exoccipital

As discussed by Vari (1983:38–41, figs. 33–35), both the Prochilodontidae and the Curimatidae have significantly expanded the plesiomorphic cul-de-sac on the posterior surface of the exoccipital into which the anterior portion of the scaphium inserts. As a result, the opening in the these families is no longer a relatively small cul-de-sac but is instead a large foramen that is continuous anterolaterally with the lateral occipital foramen and anteriorly with the interior of the neurocranium. This condition of the exoccipital is unique to the Prochilodontidae and Curimatidae within the Characiformes and consequently was hypothesized by Vari (1983) to be derived. These restructurings of the exoccipital were found to be universal within the Prochilodontidae in this study, confirming the modifications as a synapomorphy for the clade formed by that family plus the Curimatidae.

The Curimatidae plus Prochilodontidae also were reported by Vari (1983:39–40) to share the posterior expansion of the exoccipital lateral to the foramen magnum thereby forming a common aperture for the foramen magnum, cavum sinus imparis, and paired fossae for the scaphium. This expansion is best demonstrated by a consequent lateral overlap of the anterolateral portion of the scaphium by the posteriorly expanded exoccipital. Such a posterior expansion of this portion of the exoccipital was found in all species of the Prochilodontidae examined in this study, and following the evidence discussed by Vari (1983), it is considered to be a synapomorphy for the clade formed by the Prochilodontidae plus Curimatidae.

MYOLOGY

Vari (1983:45, fig. 39) hypothesized that two features of the adductor mandibulae muscle were synapomorphic for the members of the Prochilodontidae. The first of these involves the posterior extension of the A_1 portion of the adductor mandibulae. As a consequence, that muscle has a broad insertion not only on the horizontal arm of the quadrate, but also on the horizontal arm of the preopercle and to the central portion of the vertical arm of the preopercle. An examination of a broader range of prochilodontids than was available to Vari (1983) has revealed that this expansion is general among all examined taxa.

CHARACTER 111. Degree of development of A_1 portion of adductor mandibulae muscle. State 0: Muscle arises mostly, if not completely, from lateral process of quadrate; State 1: Muscle arises not only from quadrate, but also from horizontal arm of preopercle and central portion of vertical arm of preopercle.

Associated with the posterior expansion of the A_1 portion of the adductor mandibulae is the exclusion of the A_2 portion of that muscle from its plesiomorphic area of attachment along the horizontal limb of the preopercle and ventral region of the vertical limb of that ossification. As noted by Vari (1983:45), the A_2 portion of the adductor mandibulae is consequently significantly reduced. Broader comparisons in this study indicate that these features are present in all examined prochilodontids.

CHARACTER 112. Area of origin of A_2 portion of the adductor mandibulae. State 0: Horizontal limb and ventral portion of vertical limb of preopercle; State 1: Limited region of vertical limb of preopercle.

PIGMENTATION

Phylogenetically informative pigmentation characters are discussed by major regions: head, body, and fins.

Head

Prochilodus species have a field of brown or black chromatophores that form an irregular mark on the upper half of the opercle (see Figures 32, 35, 39, 40, 44–47, 51, 53, 57–59). Such a pigmentation pattern is absent in both *Ichthyoelephas* and *Semaprochilodus* and within proximate outgroups to the Prochilodontidae. The possession of such pigmentation on the opercle in the species of *Prochilodus* is, thus, considered to be derived.

CHARACTER 113. Patch of dark pigmentation on upper half of opercle. State 0: Absent; State 1: Present.

Semaprochilodus species all have black or dark brown pigmentation on the membranous border of the opercle and on the lateral exposed portion of the pectoral girdle. No comparable dark pigmentation occurs in the other members of Prochilodontidae or within proximate outgroups to that family. The possession of that feature is hypothesized to be a synapomorphy for the members of the genus. Within *Semaprochilodus* the pigmentation on the membranous border of the opercle and lateral exposed portion of the pectoral girdle is particularly intensely pigmented in three species (*S. brama, S. laticeps, S. varii*) in which it forms a distinct, very dark band. This is hypothesized to be a further derived condition, given the lack of such intense pigmentation in this region in proximate outgroup taxa.

CHARACTER 114. Dark pigmentation on membranous border of opercle and lateral exposed portion of pectoral girdle. State 0: Absent; State 1: Moderately to intensely darkly pigmented; State 2: Intensely darkly pigmented.

Body

The species of *Ichthyoelephas* have a blotch of black pigmentation that forms an irregular pigment patch on the fourth through seventh scales of the lateral-line series and on the third and fourth scales of the scale row that runs immediately ventral to the lateral line (Figures 29, 31). Given the absence of such pigmentation in the remainder of the Prochilodontidae and among proximate outgroups, we hypothesize that the presence of that feature is derived.

CHARACTER 115. Dark pigmentation on fourth through seventh scales of lateral line and third and fourth scales of scale row just ventral of lateral line. State 0: Absent; State 1: Present.

Nine species of *Prochilodus* (*P. argenteus, P. brevis, P. costatus, P. hartii, P. lacustris, P. lineatus, P. mariae, P. nigricans, P. rubrotaeniatus*) have wavy, dark, horizontal stripes on the lateral surface of the body (Figures 32, 35, 40, 44–46, 51, 53, 58). These stripes are formed by concentrations of melanophores along the dorsal and ventral margins of the exposed portions of the scales in that region. The number of dark stripes varies both within and between species within this subunit of the Prochilodontidae. In the case of *P. hartii*, most specimens demonstrate the dark body stripes; however, the largest examined individuals do not demonstrate this pattern because the body pigmentation in these specimens is masked by large amounts of guanine that remain on the scales. An examination of additional large specimens of *P. hartii* that lack such guanine is necessary to determine whether that species undergoes an autapomorphic ontogenetic loss of the dark stripes on the body.

A pattern of dark stripes that extend along the boundary between the dorsal and ventral margins of the scales on the body also characterizes all species of *Semaprochilodus*. In most *Semaprochilodus* species, the pigmentation clearly forms wavy irregular stripes, but the stripes are interrupted in some individuals (see Figures 60, 62, 67, 68, 70, 71). The relatively numerous and consequently smaller scales of *S. taeniurus* cause the margins on the dark stripes to appear to be more uniform than in congeners, but close examination reveals the same irregular margins that occur in other species of *Semaprochilodus*.

Dark pigmentation along the dorsal and ventral margins of the body scales is absent in *Prochilodus britskii, P. magdalenae, P. reticulatus, P. vimboides*, and both species of *Ichthyoelephas*. Such pigmentation also is absent in the members of the first outgroup to the Prochilodontidae, the Curimatidae. Although some members of the second outgroup (e.g., *Pseudanos irinae;* see Winterbottom, 1980, fig. 21) have irregular dark pigmentation on the scales, that pigmentation does not form the distinct horizontal patterns in *Semaprochilodus* and most *Prochilodus* species. The possession of this form of dark body striping along the scale margins is considered to be derived within the Prochilodontidae, but under the overall most parsimonious hypothesis of intrafamilial relationships (see "Phylogenetic Reconstruction") it is hypothesized to have arisen independently in the nine cited species of *Prochilodus* and in *Semaprochilodus*.

CHARACTER 116. Dark, wavy, horizontal striping on body formed by concentrations of dark chromatophores along dorsal and ventral margins of scales. State 0: Absent; State 1: Present.

Fins

Species of *Ichthyoelephas* and *Prochilodus* have anal fins that are either hyaline or have an irregular dark pigmentation not arranged into discrete stripes. At least at some point during ontogeny all members of *Semaprochilodus* instead have one to five irregular oblique stripes that extend from the anterior margin or the base of the anterior rays of the fin across to the distal margin of the fin (see Figures 60, 62, 67, 68, 70, 71). This dark pigmentation pattern on the fins can, however, be faint or effectively absent in very large individuals of some *Semaprochilodus* species (e.g., *S. brama,* Figure 60). No such anal-fin pigmentation pattern is present among proximate outgroups to the Prochilodontidae, and the presence of that pigmentation feature uniquely within *Semaprochilodus* in the Prochilodontidae is considered to be derived.

CHARACTER 117. Dark stripes that extend across anal fin at some point in ontogeny. State 0: Absent; State 1: Present.

Species of *Semaprochilodus* have a total of five to 15 dark, well-developed stripes on the caudal fin at some point during ontogeny. Two to seven of these oblique dark stripes extend across each lobe, and one horizontal stripe overlies the middle rays of the fin (see Figures 60, 62, 67, 68, 70, 71). Although very obvious in small through most large *Semaprochilodus* specimens, these stripes are often faint or occasionally absent in very large individuals of some species (e.g., *S. brama,* Figure 60). Dark caudal-fin stripes are absent in other members of the Prochilodontidae, with the only other dark caudal-fin pigmentation present among prochilodontids being chevron-shaped dark marks that characterize a subset of *Prochilodus* species (see discussion of Character 119), a very different and apparently nonhomologous pigmentation pattern. Among proximate outgroups to the Prochilodontidae such dark caudal-fin stripes are absent in the Curimatidae, the first outgroup; within the second outgroup, which consists of the families Chilodontidae and Anostomidae, such pigmentation only occurs in the anostomid genus *Leporellus* (see Géry, 1977:153). The stripes of *Leporellus* differ, however, from those present in *Semaprochilodus* in the degree to which they extend across the lobes of the fin. Furthermore, because of the phylogenetic distance between the species of *Semaprochilodus* and *Leporellus,* the possession of these features in the two genera is considered to be homoplastic, and the presence of such caudal-fin stripes in *Semaprochilodus* is consequently considered to be synapomorphic for the species of that genus.

CHARACTER 118. Dark stripes that extend across caudal fins at some point in ontogeny. State 0: Absent; State 1: Present.

Intrafamilial variation in the presence of dark pigmentation on the caudal fin also is phylogenetically informative within *Prochilodus*. The caudal-fin lobes bear two to eight irregular, vertical, somewhat chevron-shaped bars formed of small black marks in five *Prochilodus* species (*P. brevis, P. lacustris, P. mariae, P. nigricans, P. rubrotaeniatus;* see Figures 35, 45, 51, 53, 58). This pigmentation differs significantly in arrangement and distribution from the aforementioned dark caudal-fin pigmentation present in *Semaprochilodus*. Such a dark caudal-fin pigmentation pattern comparable to that present in these five *Prochilodus* species was not found in examined species of the proximate outgroups to the Prochilodontidae, and this pattern is consequently considered to be derived.

CHARACTER 119. Irregular, vertical, somewhat chevron-shaped bars formed of small black marks on caudal fin. State 0: Absent; State 1: Present.

PROCUMBENT DORSAL-FIN SPINE

All species of the Prochilodontidae have the dorsal fin preceded by an anteriorly expanded procumbent spine (Figure 23A). The position of the spine corresponds with the small fin-ray present anterior of the dorsal-fin base in many members of the Characiformes, including proximate outgroups to the Prochilodontidae, and the two features are considered to be homologous. Two aspects of the procumbent spine in the Prochilodontidae are hypothesized to be derived: its proportionally large size relative to the small fin-ray that is present in that position in proximate outgroups; and its development of either a simple or bifurcate anteroventral process.

Procumbent spines are unknown in the second outgroup (Anostomidae plus Chilodontidae) to the Prochilodontidae. Furthermore, the only species in the first outgroup (Curimatidae) with modification of the originally small fin ray anterior to the dorsal fin that is comparable to that in the Prochilodontidae is *Cyphocharax abramoides* (see Vari, 1992:18, fig. 2), an unusually deep-bodied member of the Curimatidae. *Cyphocharax* is, however, deeply nested within the phylogeny of the Curimatidae (Vari, 1989a, fig. 44), making it most parsimonious to conclude that the derived occurrence of this modification of the first dorsal-fin ray in *Cyphocharax abramoides,* on the one hand, and the Prochilodontidae, on the other, is homoplastic.

Looking beyond the first and second outgroups to the Prochilodontidae, we find that procumbent spines derived from the small first ray of the dorsal fin are known elsewhere in the Characiformes only in the subfamily Stethaprioninae of the family Characidae (see Reis, 1989:10, figs. 7–11). The Characidae is distant phylogenetically from the Prochilodontidae (Vari, 1983; Buckup, 1998), and the occurrence of procumbent

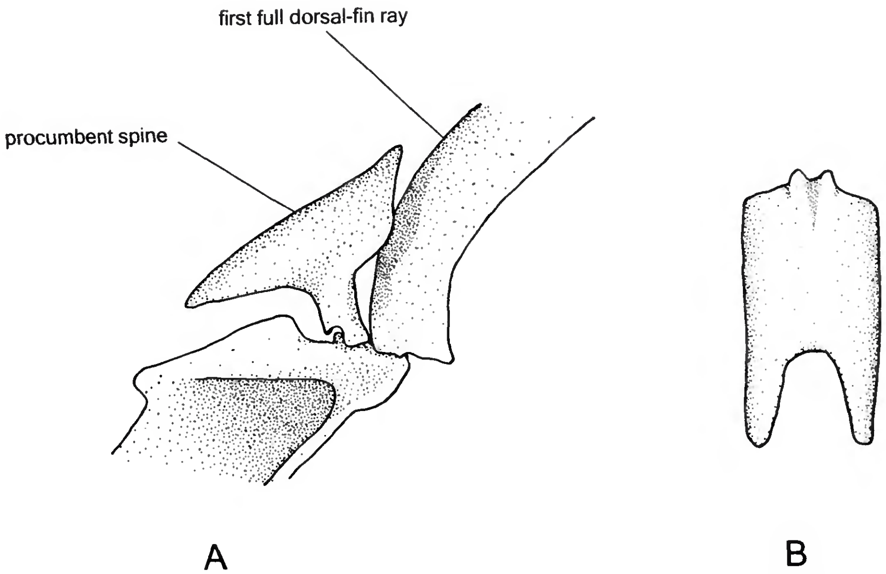


FIGURE 23.—Procumbent dorsal-fin spine: A, lateral view in *Prochilodus rubrotaeniatus*, USNM 225419, showing position relative to adjoining ossifications; B, anterodorsal view in *Prochilodus nigricans*, USNM 231438.

spines in components of these two families is considered to be homoplastic.

The spine-like process anterior to the base of the dorsal fin in the characid subfamily Serrasalminae is a portion of the basal pterygiophore rather than an independent element. As such, this structure in the Serrasalmine is nonhomologous with the various forms of procumbent spines present in the Prochilodontidae and Stethaprioninae.

CHARACTER 120. Well-developed, procumbent, dorsal-fin spine. State 0: Absent; State 1: Present.

In the species of *Ichthyoelephas*, the procumbent spine is approximately triangular in lateral view, but it is only moderately transversely expanded and has the anteroventral portion of the spine undivided. The species of *Prochilodus* and *Semaprochilodus*, in contrast, have the anterior portion of the spine both more transversely developed and also anteriorly bifurcate (Figure 23B). Because of the absence of a procumbent predorsal spine in almost all species of the first outgroup, the Curimatidae (with one exception, *Cyphocharax abramoides;* see above), including basal lineages in that family, and in all components of the second outgroup, it is impossible to evaluate which of the two forms of the procumbent spine present in the Prochilodontidae is plesiomorphic for the family. The character is consequently coded as unknown for the outgroup. The most parsimonious hypothesis of relationships indicates that it is equally parsimonious to hypothesize that the anterior forking of the procurrent spine arose in the ancestral prochilodontid and was secondarily lost in *Ichthyoelephas* or that it arose independently in both *Prochilodus* and *Semaprochilodus* (see "Phylogenetic Reconstruction"). In order to maximize homology propositions, we follow de Pinna (1991) and accept the first of these hypotheses for the purposes of the phylogeny reconstruction.

CHARACTER 121. Form of procumbent dorsal-fin spine. State 0: ?; State 1: Anteriorly undivided; State 2: Anteriorly divided.

SCALES

At a gross morphological level, the most distinctive attribute of the scales within the Prochilodontidae involves the fleshy posterior portions of the middorsal scales between the posterior of the dorsal fin and the anterior of the adipose fin in *Ichthyoelephas* and *Semaprochilodus*. In *Prochilodus*, the scales in that region have a very slightly developed fleshy margin similar to that present in many characiforms. In *Ichthyoelephas* and *Semaprochilodus*, each scale of the middorsal region between the dorsal and adipose fins has a well-developed, posteriorly rounded, fleshy flap that significantly overlaps the dorsal surface of the succeeding scale. The scales of the horizontal series that flank the middorsal scales on each side often have shorter fleshy flaps that are asymmetrically more developed on the dorsal side of the scale that borders the middorsal scale series. Outgroup comparisons have not revealed such modifications of the middorsal and adjoining scales elsewhere within the Characiformes, and their possession is consequently considered to be a synapomorphy for *Ichthyoelephas* plus *Semaprochilodus*.

CHARACTER 122. Well-developed, posteriorly rounded, fleshy flap on scales in middorsal region between posterior of dorsal fin and anterior of adipose fin and sometimes less devel-

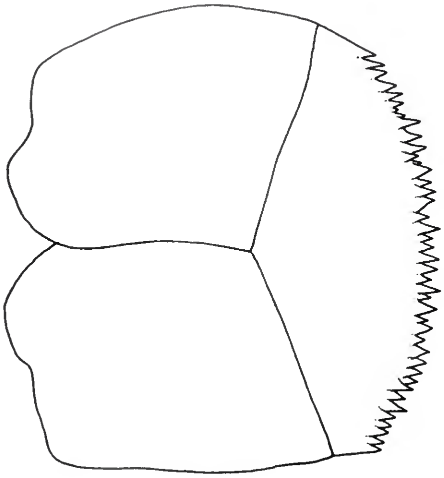


FIGURE 24.—Scale form in *Prochilodus mariae*, USNM 258164, showing the spinoid processes characteristic of the genus; radii of scales not illustrated.

oped asymmetrical series of flaps on adjoining scales in that region. State 0: Absent; State 1: Present.

Variation in the form of the posterior margin of the scales among prochilodontids have been used as generic features. Various authors (e.g., Eigenmann, 1912:270; Mago-Leccia, 1972:44) reported "ctenoid" scales (=spinoid scales of this study; see "Methods and Material") in the species of *Prochilodus* (Figure 24) that they contrasted with the cycloid scales of both *Ichthyoelephas* and *Semaprochilodus*. In his analysis of the morphology of spined scales in the Teleostei, Roberts (1993:61) noted that the term ctenoid has been applied to a diversity of different types of scales that had in common various spine-like projections on the posterior field of the scale, or that have irregular margins to the scale. Roberts (1993) highlighted the fact that such scale processes in different groups of fishes were the consequence of diverse modifications of the posterior region of the scale and as such did not represent homologous structures. Following Johnson (1984) who recognized "true" cteni that are formed by separate ossifications, Roberts (1993:70, fig. 6e,f) restricted the term "ctenoid" to scales with such separate marginal ossifications. Although a variety of taxa in the Characiformes, including *Prochilodus*, were previously considered to have ctenoid scales, under the more exact definitions proposed by Johnson (1984) and Roberts (1993), ctenoid scales (i.e. with cteni formed by separate ossifications) are limited to the family Distichodontidae within that order (see Vari, 1979, fig. 38; Roberts, 1993, fig. 7). Roberts (1993) identified the different type of scale found in *Prochilodus* as spinoid, the term he utilized to characterize all scales that have the spines projecting posteriorly as continuations of the main body of the scale.

In *Prochilodus nigricans*, the spines of the spinoid scales "grow in approximately alternating rows forming small flat spines marginally and remnants submarginally that have fused into the posterior field" (Roberts, 1993:70). This description applies to all members of the genus, although there is variation in the degree of development of the spines among and within different species of *Prochilodus*. Among the proximate outgroup to the Prochilodontidae, distinct spines on the scales occur in some curimatids (*Potamorhina pristigaster*, see Roberts, 1993, fig. 6a,b; *Psectrogaster curviventris*, see Cockerell, 1914, pl. 23), whereas other species in the Curimatidae have irregular posterior margins on the scales (e.g., *Curimatus* (= *Cyphocharax*) *microcephalus*, see Cockerell, 1914, pl. 25: fig. 5). The form of the spines in the cited curimatids significantly differ, however, from those in *Prochilodus* (Figure 24); thus, they are considered to be nonhomologous developments of irregular posterior margins to the scales. All remaining curimatids have cycloid scales (e.g., *Curimatus* (= *Cyphocharax*) *spilurus*; see Cockerell, 1914, pl. 25: fig. 4) as do the members of the secondary outgroup, the Anostomidae (see Winterbottom, 1980, fig. 7) and Chilodontidae. Because of its unique nature within the Prochilodontidae and at least proximate outgroups, the spinoid form of scale in *Prochilodus* is considered to be a synapomorphy for the members of the genus.

CHARACTER 123. Form of scales. State 0: Not as in State 1; State 1: With alternating rows that form small flat spines marginally and remnants submarginally that have fused into the posterior field.

One of the noteworthy features of the scales in all prochilodontids is the arrangement of the radial subdivisions of the scales, which are clearly illustrated in Roberts (1993, fig. 5e) for the scales of *Prochilodus nigricans*. Although no such modifications of the scales occur in the Curimatidae (e.g., *Potamorhina pristigaster*, see Roberts, 1993, fig. 6a; *Psectrogaster curviventris*, see Cockerell, 1914, pl. 23), they are present in the members of the Chilodontidae and Anostomidae (Winterbottom, 1980, fig. 7), and the possession of these radial subdivisions is consequently considered to be plesiomorphic for the members of the Prochilodontidae. The absence of such radial subdivisions is potentially another synapomorphy for the Curimatidae within at least the context of the clade that consists of the Anostomidae, Chilodontidae, Curimatidae, and Prochilodontidae. If so, this would supplement the nineteen synapomorphies for the Curimatidae proposed by Vari (1983:48; 1989:52).

Although radial subdivisions of the scales are universal within the Prochilodontidae, *Prochilodus nigricans* and *P. rubrotaeniatus* have a more complex pattern of generally vertical subdivisions that extend to the dorsal and ventral margins of the scales (Figure 25; see also Cockerell, 1914, pl. 24). Some of the scales in these two species have secondary subdivisions that arise from the vertical subdivisions (those that extend to the dorsal and ventral margins of the scale) to the anterior margin of the scale. There is, however, pronounced variation in the form and complexity of these secondary subdivisions between and within both *P. nigricans* (Figure 25A,B) and *P. rubrotaenia-*

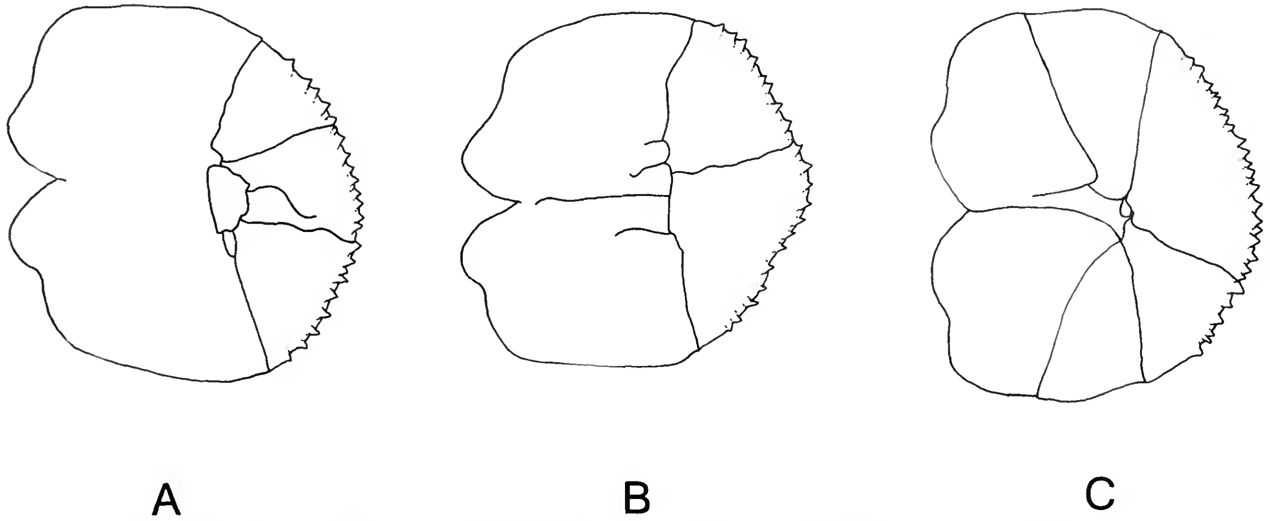


FIGURE 25.—Scales: A,B, *Prochilodus nigricans*, USNM 280447; C, *Prochilodus rubrotaeniatus*, USNM 225419, showing some of the variation of the secondary subdivisions within the scales.

tus (Figure 25C) and indeed even between scales taken from a single specimen. Furthermore, some scales in individuals of each species completely lack the complex secondary pattern (e.g., the scale of *P. nigricans* illustrated by Roberts, 1993, fig. 6e). The more complex pattern of scale subdivisions found in these two species has not been found in other prochilodontids. As noted above, the Curimatidae, the first outgroup, lacks internal subdivisions to the scales, and examined species of the Chilodontidae, one component of the second outgroup, have simple radial subdivisions of the scales. Although most members of the Anostomidae have simple subdivisions of the scales, some components of the subfamily Anostominae have complex subdivisions of the scales (see Winterbottom, 1980, fig. 7e). Those taxa are, however, phylogenetically distant from *P. nigricans* and *P. rubrotaeniatus* (Winterbottom, 1980; Vari, 1983; herein), and the presence of subdivisions in those anostomines is most parsimoniously regarded as homoplastic with respect to the presence of the similar feature in these two *Prochilodus* species. The more elaborate pattern in these two *Prochilodus* species is, thus, hypothesized to be derived.

CHARACTER 124. Complex pattern of variable accessory subdivisions and included islands within scales. State 0: Absent; State 1: Present.

Phylogenetic Reconstruction

The phylogenetic analysis in this study is focused on two interrelated issues; assessing the monophyly of the Prochilodontidae and defining the species-level relationships within that family. In the process of addressing those questions, an additional hypothesized synapomorphy for the clade that consists of the Prochilodontidae, Curimatidae, Anostomidae, and Chilodontidae was identified, and we reevaluated the characters proposed by Vari (1983) as synapomorphies for the clade formed by the Prochilodontidae and Curimatidae. The previously proposed synapomorphies at both suprafamilial levels of inclusiveness had been based upon observations on a subset of the species in the Prochilodontidae; their presence across the Prochilodontidae was confirmed herein. Those characters pertinent to these clades are summarized below but are not included in the phylogenetic analysis because the question of the monophyly of these two clades lies outside of the scope of this study.

MONOPHYLY OF THE PROCHILODONTIDAE, CURIMATIDAE, ANOSTOMIDAE, AND CHILODONTIDAE CLADE

The Prochilodontidae, Curimatidae, Anostomidae, and Chilodontidae are hypothesized to form a clade within the Characiformes on the basis of their possession of five synapomorphies (Figure 26), four of which (A to D) were previously proposed by Vari (1983:46), whereas the fifth (E) was discovered during this study:

The elimination of the direct contact between the fourth and fifth upper pharyngeal tooth plates.

The absence of dentition on the fourth upper pharyngeal tooth plate.

The A3 portion of the adductor mandibulae with an extensive origin along the lateral surface of the mesopterygoid and metapterygoid and a broad insertion on the tendon of A2.

The longitudinally expanded attachment of the hyohydoidei abductores on the urohyal.

The absence throughout ontogeny of dentition implanted on the maxilla (see discussion under "Oral Dentition," above).

MONOPHYLY OF THE PROCHILODONTIDAE AND CURIMATIDAE CLADE

A hypothesis of the monophyly of the clade formed by the Prochilodontidae plus Curimatidae was advanced by Vari (1983:47) and was based upon 11 proposed synapomorphies. In a subsequent publication, Vari (1989a:51) proposed another four synapomorphies for the two-family clade, for a total of 15 characters (Figure 26). These synapomorphies, previously discussed in detail by Vari (1983, 1989a), and whose presence was confirmed for all members of the Prochilodontidae in this study, are as follows:

The reorientation of the dorsal process of the fourth epibranchial anteriorly with its resultant extension over the dorsal surface of the fourth infrapharyngobranchial (see Vari, 1989a, figs. 5–13).

The anterodorsal expansion of the cartilaginous fifth epibranchial, its attachment to the posterodorsal margin of the fourth epibranchial, and the resultant encirclement of the fifth efferent branchial artery by those bones and cartilages (see Vari, 1989a, figs. 5, 6, 8–11).

The large, sac-like, muscular epibranchial organ that extends dorsal to the medial elements of the dorsal portions of the gill arches (see Menin and Mimura, 1991, fig. 1).

The conversion of the plesiomorphously flat fourth upper pharyngeal tooth plate into a curved ossification that wraps around the ventral, lateral, and medial surfaces of the fourth infrapharyngobranchial (see Vari, 1989a, figs. 5, 6, 8–16).

The reduction or loss of the dentition on the ventral surface of the fifth upper pharyngeal tooth plate (see Vari, 1989a, figs. 5, 7–11).

The reduction (Curimatidae) or loss (Prochilodontidae) of an ossified first basibranchial (see Vari, 1983, fig. 9; 1989a, fig. 25).

The absence of dentition on the dorsal surface of the fifth ceratobranchial except in very small specimens (see Vari, 1989a, figs. 25, 27).

The anteromedially directed process on the ventral surface of the fourth ceratobranchial (see Vari, 1989a, fig. 6).

The distinct posteroventrally aligned flange on the lateral surface of the opercle (Curimatidae) or a further derived condition of that process (Prochilodontidae) (see Vari, 1983, fig. 27).

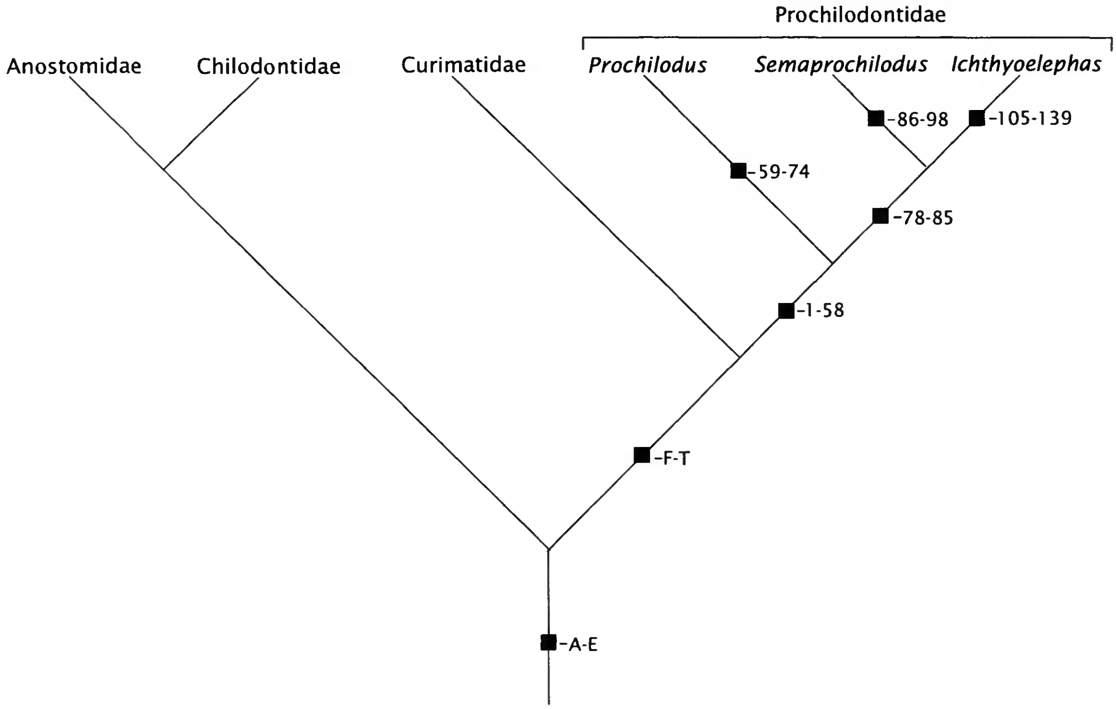


FIGURE 26.—Cladogram of the most parsimonious hypothesis of relationships for and within the Prochilodontidae (lettered and numbered synapomorphies correspond to those of the text). Cladograms for species within *Prochilodus* and *Semaprochilodus* presented in Figures 27 and 28, respectively. Synapomorphies for the clade formed by the Anostomidae plus Chilodontidae and for the clade consisting of the Curimatidae were discussed by Vari (1983, 1989a, respectively).

The increase in the depth and width of the fossa for the scaphium that results in the interconnections of the fossa with the lateral occipital foramen laterally and the interior of the cranium anteriorly (see Vari, 1983, fig. 34).

The posterior development of the lateral margin of the exoccipital lateral to the foramen magnum, and the consequent formation of a common aperture for the foramen magnum, the cavum sinus imparis, and the paired fossae for the scaphium. The anteriorly expanded exoccipital consequently forms a cover laterally for the anterolateral surface of the scaphium (see Vari, 1983, fig. 33).

The constriction of the complex formed by the fourth infrapharyngobranchial and fourth upper pharyngeal tooth plate that results in a convex lateral margin to those conjoined elements (see Vari, 1989a, figs. 15, 16).

The expansion and restructuring of the uncinate process of the third epibranchial into an anterior process that overlies the line of articulation between the third infrapharyngobranchial and third epibranchial (see Vari, 1989a, fig. 19).

The subdivision of the anterior articular surface of the third epibranchial with the expansion and reorientation of the ossified medial portion of the articulation into a medially directed ossified process that extends along a matching groove on the anterodorsal portion of the fourth infrapharyngobranchial (see Vari, 1989a, figs. 5, 6, 8–11, 19).

The expansion of the posterolateral portion of the third infrapharyngobranchial into a distinct dorsal flange (see Vari, 1989a, figs. 5, 6, 8–11).

The form of the drumming muscle (the Trommenmuskel of Dorn, 1972) on the anterior-most ribs and the anterior portion of the swimbladder that is associated with sound production in males of both the Curimatidae (*Potamorhina altamazonica,* Dorn, 1972:170, fig. 1; Schaller, 1974:249 (species cited therein as *Anodus laticeps*)) and Prochilodontidae (*Semaprochilodus insignis,* Schaller, 1971:573, 1974:249, unnumbered fig. (species cited therein as *Prochilodus insignis*) and *P. nigricans* (Schaller, 1974:249)) likely represent a series of additional synapomorphies for these two families. Preliminary investigations indicate that the sound-producing system in these two families involves not only the development of drumming muscles that are absent in other characiforms, but also modifications of the first rib. The characterization of the derived attributes in this system requires, however, the analysis of a larger series of specimens than was available for this study, and this feature is consequently not formally utilized as a synapomorphy in this analysis.

MONOPHYLY OF THE CURIMATIDAE

Vari (1983:48, 1989a:52) proposed a total of 19 synapomorphies for the Curimatidae. Outgroup comparisons performed in this study yielded two other potential synapomorphies for the family. The first of these is the reduction, or absence, in the Curimatidae of the anterior process of the lateral ethmoid that extends anteriorly in many characiforms to contact the mesethmoid or vomer (see discussion under "Lateral Ethmoid," above). The second of these is the apparent absence of radial subdivisions of the scales in the Curimatidae (see discussion under "Scales," above). Confirmation of these characters as synapomorphies for the Curimatidae requires examination of all members of the family, an endeavor beyond the limits of this study.

MONOPHYLY AND INTRAFAMILIAL PHYLOGENY OF THE PROCHILODONTIDAE

The analysis, using the "ie" option in Hennig 86, yielded a single tree with a consistency index of 0.98 and a retention index of 0.99. These values reflect the heavy loading of characters at major nodes with little discrete variation in examined characters interspecifically (see also "Bauplan Shifts and Stasis," below).

The evidence from the phylogenetically informative character systems pertinent to the question of the monophyly of the Prochilodontidae and the interrelationships within that family is summarized below and in Figures 26 to 28. The number in parentheses after each of the proposed synapomorphies corresponds to the numbering of the characters in the preceding "Character Descriptions and Analysis."

MONOPHYLY OF THE PROCHILODONTIDAE

In his study of the relationships of the Prochilodontidae, Curimatidae, Anostomidae, and Chilodontidae, Vari (1983:49) listed 18 shared derived characters for the Prochilodontidae. Further analysis of all, rather than a subset, of the species in the Prochilodontidae confirmed the derived nature of all of these characters, but it also demonstrated that in some instances the characters as defined by Vari (1983) subsume several intrafamilially phylogenetically variable features informative at lower levels of generality. In those instances, the character complex as defined by Vari (1983) was subdivided in this analysis into two or more characters as appropriate. Some of the features in the following listing were first cited in less detail by Vari (1983), as noted in the parenthetical comments.

In the following list and on Figure 26 the synapomorphies for the Prochilodontidae are arranged in the sequence of their description in the "Character Descriptions and Analysis." This list includes both those synapomorphies proposed by Vari (1983), which were confirmed and in some cases redefined herein, and those synapomorphies first identified in this study. The number in parentheses after the description of each synapomorphy corresponds to the number of the character presented in the character discussion and is in certain instances followed by comments on optimization or secondary loss. Only two of the characters (1, 3) demonstrate homoplasy, and the others have a ci of 1.0. Autapomorphies for a species are not noted in the character discussion unless they are one component of a multi-state character.

1. The expansion of the first infrapharyngobranchial with the resultant contact of that ossification with the anterior portion of the second epibranchial (first epibranchial absent as an ossified element in *Ichthyoelephas*) (2).
2. The posterolaterally oriented process that extends from the base of the uncinate process of the first epibranchial into the trough-like central portion of that ossification (5).
3. The expansion of the fourth upper pharyngeal tooth plate beyond the condition in the Curimatidae to partially to totally envelope the dorsal surface of the fourth infrapharyngobranchial (secondarily reduced in *Ichthyoelephas*) (10).
4. The transverse compression of the fifth upper pharyngeal tooth plate and the distinct mobility of that element relative to the fourth epibranchial (12).
5. The transverse expansion of the anterior portion of the basihyal (14).
6. The ventrally notched interhyal and the presence of a sesamoid ossification in the ligament that joins the interhyal to the posterior ceratohyal (17).
7. The transverse broadening of the branchiostegal rays (18).
8. The highly developed transverse widening of the ventral wings of the urohyal (19).
9. The implantation of the teeth of the upper and lower jaws on the fleshy lips rather than directly onto the dentary and premaxilla (20).
10. The distinct separation anteromedially of the two rows of teeth in each jaw (21).
11. The possession of 8 to 76 teeth on each side in the inner tooth row of the upper jaw and 4 to 70 teeth on each side in the inner tooth row of the lower jaw (22).
12. The possession of 2 to 22 rows of replacement teeth in both the upper and lower jaws (23).
13. The possession of elongate, curved or falcate teeth with a distinct orientation towards the bucco-pharyngeal cavity (24).
14. The enlarged and highly developed fleshy lips that are broadly in contact posteriorly and form a suctorial oral disk, and the lack of direct attachment of the posterior portions of the lip to the adjoining lateral portions of the jaws (25).
15. The presence of a ledge-shaped process on the lower lip formed of stiff connective tissue under the margin of the lower lip (26).
16. The shift of the upper jaw to a more medial position relative to adjoining ossifications, with the lateral surface of the maxilla mostly overlapped by the first infraorbital in the closed mouth (28).
17. The increased mobility between the premaxilla and mesethmoid with resultant anteroposterior motion of the premaxilla with respect to the mesethmoid (29).
18. The possession of a discrete, approximately tubular mass of connective tissue in region of the junction of the premaxilla, maxilla, and palatine (30).
19. The restructured anteromedial portion of the premaxilla with a twisting form anteriorly and with the posterior portion distinctly laterally convex in cross section, with the medial portion of the contralateral premaxilla shifted to ventral of the anterior articular portion of the mesethmoid (= the bulbous form of the premaxilla of Vari, 1983) (31).
20. The possession of a well-developed ligament that extends between the posteromedial surface of the anteroventral process of the premaxilla and the medial surface of the posterior portion of the premaxilla (34).
21. The distinctly laterally convex maxilla in both the horizontal and vertical axes, with the posterior portion of the bone helmet shaped from lateral view (35).
22. The thickening of the posterior portion of the maxilla and the development of dorsal and ventral projections on that portion of the bone (36).
23. The presence of a series of foramina that extends through the posterior portion of the maxilla (38).
24. The presence of a moderate to large foramen through the maxilla slightly posterior of where the rear margin of the premaxilla extends over the maxilla (40).
25. The possession of a highly developed process on the maxilla onto which the primordial ligament attaches (41).
26. The foreshortened dentary and the expanded, laterally rotated dentary replacement tooth trenches that is continuous across the dentary symphysis, at least to a limited degree (47).
27. The large, horizontally elongate or rounded opening in the rear wall of the replacement tooth trench of the dentary (49).
28. The shortened laterosensory canal segment in the dentary limited to the posterior one-half of the horizontal extent of the bone (50).
29. The medial shift of the bony process at the posteroventral corner of the dentary (51).
30. The presence of the bony process that arises from the medial surface of the dentary and that overlaps the medial surface of the coronomeckelian cartilage (52).
31. The anterodorsally aligned laterosensory canal in the angulo-articular oriented at a distinct angle relative to the laterosensory canal segment in the dentary (56).
32. The lateral separation of the dorsal portion of the angulo-articular from the adjoining region of the dentary, with the intervening space occupied by a dense connective tissue mass (57).

33. The large foramen on the lateral surface of the angulo-articular anterodorsal to the articular facet (58).
34. The proportionally relatively small retroarticular with laterally concave form that is positioned on the anteromedial surface of the angulo-articular (59).
35. The attachment of the primordial ligament onto a highly developed, lever-like process that arises from the anteromedial surface of the maxilla (61).
36. The anterior expansion of the first infraorbital to nearly contact the nasal, and the pronounced medial curvature of the first infraorbital with the development of a medial ridge along its dorsomedial portion (62).
37. The presence of a series of small ramifying canals in the first infraorbital (63).
38. The presence of a distinct indentation of the anterior portion of the second infraorbital (66).
39. The development of a distinct anterodorsal process on the second infraorbital that carries the laterosensory canal segment in the anterior portion of that bone (67).
40. The presence of two or more side branches that arise from the ventral margin of the laterosensory canal in the third infraorbital (68).
41. The dorsally flattened palatine with a pointed anterior process and the distinct anteroposterior mobility of the palatine relative to the mesethmoid (77).
42. The possession of an anteroventral process on the ectopterygoid and the overall tripartite form of that bone (79).
43. The pronounced mobility of the ectopterygoid relative to the quadrate (81).
44. The deep horizontal notch on the posterior portion of the quadrate and the distinct vertical mobility of the quadrate relative to the preopercle (82).
45. The presence of a well-developed, lateral, shelf-like process along the lateral margin of the articular facet of the quadrate (83).
46. The pronounced mobility between the mesopterygoid and the ectopterygoid (85).
47. The division of the anterodorsal margin of the metapterygoid into a lateral portion continuous with the lateral ridge on the bone and a medial process that contacts the posterodorsal portion of the mesopterygoid (88).
48. The reduction of the cartilage-capped posterior portion of the metapterygoid (90).
49. The ontogenetic expansion of the flange on the lateral surface of the opercle into a broad, flat, thickened region on the lateral surface of that ossification (92).
50. The subdivision of the anterior portion of the preopercular laterosensory canal with the consequent development of one or more independent ossified tubes between the region ventral of the articular facet of the quadrate and the main body of the preopercle (93).
51. The presence of a shelf-like process on the medial surface of the horizontal limb of the preopercle (95).
52. The presence of a transversely widened articular surface on the anterodorsal portion of the interopercle (97).
53. The longitudinally elongate, laterally compressed ventromedial process of the mesethmoid (100).
54. The pronounced fenestration of at least the basal portion of the blade-like lateral portions of the lateral ethmoid (104).
55. The presence of a fenestra that extends between the anterior surface of the sphenotic that borders the orbital cavity and the posterior surface of the ossification in the dilatator fossa (110).
56. The posterior expansion of the A_1 portion of the adductor mandibulae (111).
57. The reduction of the A_2 portion of the adductor mandibulae (112).
58. The well-developed, procumbent, predorsal spine (120).

Within the clade defined by this series of characters, the results of the phylogenetic analysis indicate that *Prochilodus* is the sister genus to a clade that consists of *Semaprochilodus* and *Ichthyoelephas* (Figure 26). Synapomorphies for *Prochilodus* and its contained intrageneric groupings (Figure 27) are discussed first followed by the listing of synapomorphies for the *Semaprochilodus* plus *Ichthyoelephas* clade.

MONOPHYLY OF *Prochilodus*

The following sixteen synapomorphies for the thirteen species of *Prochilodus* were identified during this study:

59. The ossification of the basal portions of the gill filaments on all gill arches (1).
60. The laterally elongate form of the first infrapharyngobranchial (3).
61. The expansion of the posterolaterally oriented process that arises from the base of the uncinate process into a laterally directed, horizontally aligned, flange-like process (6; optimized as a synapomorphy for *Prochilodus* within the hypothesis of overall most parsimonious relationships herein).
62. The presence of serrations along the dorsal margin of the anterior face of the first through third epibranchials that coalesce distally ontogenetically in some instances to form porthole-like openings along the margin of the bones (7).
63. The presence of a distinct ridge-like process along the anterior surface of the uncinate process of the second epibranchial (8).
64. The expansion of the ventral portion of the fourth epibranchial into a slightly medially curving, proportionally more posteriorly elongate process (11).
65. The presence of serrae along the ventral margin of the anterior face of the first through fourth ceratobranchials that coalesce distally ontogenetically in some instances in larger individuals to porthole-like openings along the margin of the bones (13).

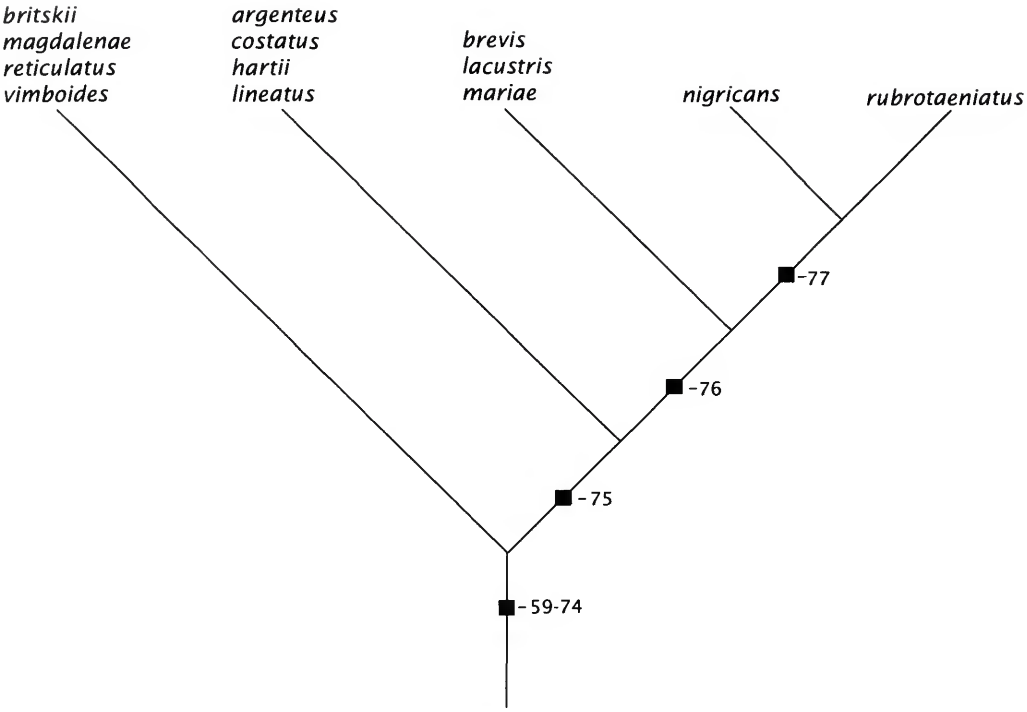


FIGURE 27.—Cladogram of the most parsimonious hypothesis of relationships within *Prochilodus* (numbered synapomorphies correspond to those of the text). Three of the groups of species (1, *P. britskii, P. magdalenae, P. reticulatus, P. vimboides;* 2, *P. argenteus, P. costatus, P. hartii, P. lineatus;* and 3, *P. brevis, P. lacustris, P. mariae*) are not defined on the basis of synapomorphies.

66. The restructuring and repositioning of the anterior portion of the coronomeckelian bone into a distinct angle with the anterior portion of the bone oriented dorsally or anterodorsally and the location of the ossification distinctly anterior to the vertical through the point where the dorsal portion of the angulo-articular passes lateral to the posterodorsal portion of the dentary (54).
67. The very close association of the retroarticular with the anteroventral surface of the angulo-articular, with the boundaries of the bones difficult to discern even in cleared and stained specimens (60).
68. The presence of highly developed, small, ramifying canals in the first infraorbital (63).
69. The presence of three or four side branches that arise from the ventral margin of the primary laterosensory canal segment in the third infraorbital (68).
70. The presence of one or two additional branches that extend anteriorly and posteriorly from the main laterosensory canal segment in the sixth infraorbital (75).
71. The reduction of the posterior portion of the mesopterygoid with a resultant posteroventral inclination to the margin of the bone (87).
72. The reduction of the anterodorsal portion of the metapterygoid with a resultant anteroventral inclination to the margin of the bone (89).
73. The presence of a field of brown or black chromatophores that forms an irregular mark on the upper half of the opercle (113).
74. The possession of spinoid scales with alternating rows that form small flat spines marginally (123).

INTERSPECIFIC RELATIONSHIPS WITHIN *Prochilodus*

The available phylogenetic evidence permits only a partial resolution of the interspecific phylogeny for *Prochilodus* (Figure 27), a situation that in retrospect is to be expected because of the restricted overall externally obvious morphological variability within the genus. At the base of the interspecific phylogeny we have a multitomy with an unresolved cluster of four species (*P. britskii, P. magdalenae, P. reticulatus, P. vimboides*) and a clade that contains the nine other species of *Prochilodus*.

The remaining nine *Prochilodus* species (*P. argenteus, P. brevis, P. costatus, P. hartii, P. lacustris, P. lineatus, P. mariae, P. nigricans, P. rubrotaeniatus*) share the following synapomorphy:

75. The presence of wavy, dark, horizontal stripes on the body (also independently acquired in *Semaprochilodus*) (116).

Within that lineage of nine species, there is an unresolved polytomy between an unresolved cluster of four species (*P. argenteus, P. costatus, P. hartii, P. lineatus*) and a clade that contains five species. *Prochilodus brevis, P. lacustris, P. mariae, P. nigricans*, and *P. rubrotaeniatus* share the following synapomorphy:

76. The presence of 2 to 8 irregular, vertical, somewhat chevron-shaped, dark bars on the caudal fin (119).

The clade defined by this synapomorphy is only partially resolved into a quadritomy that consists of *P. brevis, P. lacustris, P. mariae*, and a clade formed of *P. nigricans*, and *P. rubrotaeniatus* that share the following synapomorphy:

77. The development of radial subdivisions of the scales into a complex pattern with variable numbers of branches and irregular islands within the body of the scale (124).

MONOPHYLY OF THE *Semaprochilodus* AND *Ichthyoelephas* CLADE

The following eight synapomorphies for the *Semaprochilodus-Ichthyoelephas* clade were identified during this study (Figure 26):

78. The large foramina on the posterior portion of the maxilla (39; optimized as a synapomorphy for this clade within the hypothesis of overall most parsimonious relationships herein).
79. The distinct articular facet on the maxilla that matches the contours of the corresponding portion of the premaxilla (44).
80. The presence of a process on the dorsal margin of the maxilla that serves as an attachment area for various connective tissue bands (45).
81. The distinct ridge along the ventral margin of the expanded dentary replacement tooth trench (48; optimized as a synapomorphy for this clade within the hypothesis of overall most parsimonious relationships herein).
82. The presence of a highly developed articular surface on the anterodorsal portion of the interopercle (98; optimized as a synapomorphy for this clade within the hypothesis of overall most parsimonious relationships herein).
83. The wide anterior process of the lateral ethmoid that extends anteriorly to contact the lateral keel-like process on the ventrolateral surface of the mesethmoid (103).
84. The absence of the central portion of the ventromedial process of the orbitosphenoid that contacts the dorsomedial surface of the parasphenoid (105).
85. The possession of posteriorly elongate fleshy flaps on the posterior margins of the middorsal scales between the posterior of the dorsal fin and the anterior of the adipose fin (122).

Under the final most parsimonious analysis in this analysis, two characters (10 and 119) are hypothesized to have arisen at the level of the Prochilodontidae and reversed in *Ichthyoelephas* in order to maximize homology propositions in keeping with the practice proposed by de Pinna (1991). In both of these instances, the possession of the feature in question would be considered to be derived for *Prochilodus* and *Semaprochilodus* based upon outgroup evidence and, thus, would support a hypothesis of a sister-group relationship of those genera. A hypothesis of such a relationship is, however, less parsimonious than the hypothesis of a sister-group relationship between *Ichthyoelephas* and *Semaprochilodus* that is recognized herein on the basis of four unequivocal synapomorphies, with two additional characters optimized as synapomorphies for this clade in the final most parsimonious phylogeny.

MONOPHYLY OF *Semaprochilodus*

The following thirteen synapomorphies for the six species of *Semaprochilodus* were identified during this study (Figures 26, 28):

86. The anterior rotation of the anteroventral portion of the premaxilla into a distinct ridge in the form of a hat brim along the inner surface of the bone (33).
87. The well-developed ridge along the anterodorsal margin of the triangular process onto which the primordial ligament attaches (43).
88. The somewhat laterally bent ascending process of the maxilla (46).
89. The relatively narrow third infraorbital (69).
90. The reduction of the dorsal portion of the fifth infraorbital to a bony tube or a bony tube with limited flanges, with the dorsal tip of the fifth infraorbital falling short of the sixth infraorbital (72; optimized as a synapomorphy for the genus).
91. The more horizontally shifted orientation of the anterior portion of the supraorbital relative to the remainder of the ossification, with a distinct fold between the two regions (76).
92. The falcate form of the anteroventral process of the ectopterygoid (80; optimized as a synapomorphy for the genus).
93. The possession of a well-developed, dorsomedial ridge on the parasphenoid (106).
94. The posteromedial orientation of the junction on the dorsal surface of the cranium between the frontal and the parietal (109).
95. The presence of dark brown or black pigmentation on the membranous border of the opercle and the lateral exposed portion of the pectoral girdle (114).

96. The presence of dark, wavy, horizontal striping on the body (also independently acquired in a subgroup of *Prochilodus*) (116).
97. The presence of dark stripes that extend across the anal fin at some point during ontogeny (117).
98. The presence of dark stripes that extend across the caudal fin at some point during ontogeny (118).

INTERSPECIFIC RELATIONSHIPS WITHIN *Semaprochilodus*

As was the case with *Prochilodus,* we were able to resolve only partially the interspecific relationships within *Semaprochilodus* (Figure 28). Two clades, each of which consists of three species, can be defined by synapomorphies. The first of the clades in *Semaprochilodus* (*S. brama. S. laticeps, S. varii*) is defined by one synapomorphy:

99. The very dark pigmentation on the border of the operclum and the adjoining region of the cleithrum (114).

We were unsuccessful in discovering any characters to resolve the trichotomy within that clade.

The second clade in *Semaprochilodus* (*S. insignis, S. kneri, S. taeniurus*) is defined by two synapomorphies:

100. The vertical expansion of the articular surface of the uncinate process of the second epibranchial (9).
101. The posterior extension of the posteriorly directed branch of the laterosensory canal system in the fourth infraorbital beyond the posterior margin of the bone (70).

Within this clade of three species we have a sister-group relationships between *Semaprochilodus taeniurus* on the one hand and a clade formed by *S. insignis* and *S. kneri.* No autapomorphies have been identified for *S. taeniurus,* but *S. insignis* and *S. kneri* have been found to share two hypothesized synapomorphies:

102. The very pronounced development of the ridge on the triangular process of the maxilla onto which the primordial ligament attaches (43).
103. The loss of the suprapreopercle (99).

Of the two species in this clade, *S. kneri* does not have any identified autapomorphies, whereas *S. insignis* is characterized by one unique feature:

104. The subdivision of the vertically expanded, cartilage capped, articular surface of the uncinate process of the second epibranchial (9).

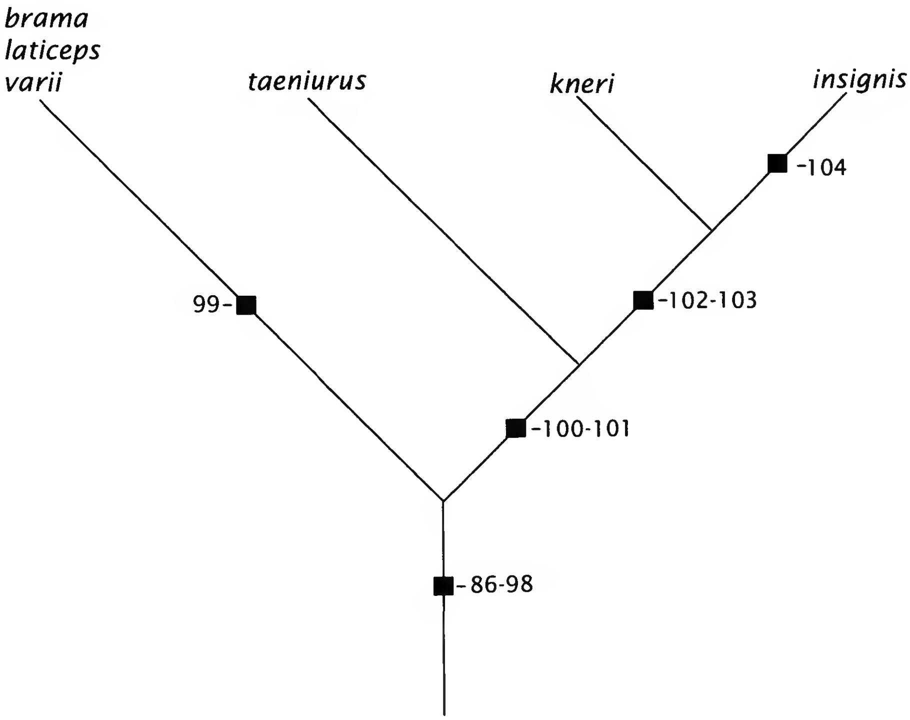


FIGURE 28.—Cladogram of the most parsimonious hypothesis of relationships within *Semaprochilodus* (numbered synapomorphies correspond to those of the text). Relationships among *S. brama, S. laticeps,* and *S. varii* have not been resolved.

MONOPHYLY OF *Ichthyoelephas*

The following synapomorphies for the two species of *Ichthyoelephas* were identified during this study (Figure 26):

105. The absence of an ossified first infrapharyngobranchial (4).
106. The secondary reduction of the fourth upper pharyngeal tooth plate such that it no longer extends onto the dorsal surface of the fourth infrapharyngobranchial (secondary reduction of optimized synapomorphy for the Prochilodontidae) (10).
107. The reduction in the degree of development of the distinct notch on the posterior margin of the dorsal hypohyal (15).
108. The absence of the distinct notch on the anterior portion of the anterior ceratohyal (16).
109. The very large fleshy upper lip that distinctly overhangs the lower lip (27).
110. The vertical expansion of the posterior portion of the premaxilla, with the development of a distinct articular surface on the posterodorsal portion of the bone where it is in contact with the maxilla (32).
111. The restructured distal margin of the maxilla into a posteroventrally angled structure with an acute posteroventral angle and the shift anteriorly of the dorsal process that caps the thickened posterior portion of the bone (37).
112. The posterior extension of the process of the maxilla that serves for the attachment of the primordial ligament (42; optimized as a synapomorphy for the genus).
113. The very well-developed, articular facet on the anterodorsal portion of the maxilla that matches the contours of the corresponding portion of the premaxilla (44).
114. The highly foreshortened dentary with very broad dentary replacement trenches that are almost continuous across the dentary symphysis (47).
115. The vertical orientation of the compact medial process of the dentary that overlaps the medial surface of the coronomeckelian cartilage and the contact of this dentary process with the ventral portion of the coronomeckelian bone (53; optimized as a synapomorphy for the genus).
116. The distinctly concave coronomeckelian bone set into a depression on the medial surface of the dentary with the coronomeckelian bone having an articular process that contacts the dorsally directed medial process of the dentary (55).
117. The deep indentation of the posterior of the first infraorbital that receives the anterodorsal tubular portion of the second infraorbital (64).
118. The presence of a series of secondary canals and multiple openings off the primary laterosensory canal in the first infraorbital (65).
119. The very deep indentation of, and acute triangular anteroventral process on, the second infraorbital (66).
120. The presence of a distinct notch along the posterior margin of the fourth infraorbital in the region where the posterior branch of the laterosensory canal contacts the rear of that ossification (71).
121. The presence of a shelf-like bony process that extends from the dorsal portion of the main laterosensory canal segment in the fifth infraorbital and the presence of a series of small apertures that arise from the posterior margin of that canal (73).
122. The presence of a series of small ramifying canals that exit from the main segment of the laterosensory canal segment in the sixth infraorbital (74).
123. The presence of a distinct medial process on the ventral portion of the palatine (78).
124. The pronounced lateral expansion of the ventral shelf-like portion of the quadrate to the vertical plane through the lateral margin of the articular facet of the quadrate (83).
125. The posterodorsal alignment of the posterior portion of the quadrate medial of the preopercle and the contact of that process with the symplectic (84).
126. The possession of a mesopterygoid that is significantly smaller than the metapterygoid (86).
127. The shortened symplectic that barely attains, or falls short of, the limits of the posteriorly and posterodorsally oriented processes on the posterior portion of the quadrate and is situated distinctly anterior of vertical through the area of attachment of the interhyal on the preopercle (91).
128. The highly developed, ramifying laterosensory canal system at the angle of the preopercle (94).
129. The well-developed, shelf-like ridge on the medial surface of the preopercle (96; optimized as a synapomorphy for the genus).
130. The wide anterior portion of the mesethmoid that is more than twice the width of the frontal portion of the cranial fontanelle (101).
131. The large, horizontally rounded anterior portion of the vomer that contacts both the anterior process and the main body of the lateral ethmoid (102).
132. The total absence of the ventral process of the orbitosphenoid (105).
133. The median contact of the posterior portions of the contralateral frontals (107).
134. The medial contact of the contralateral parietals with the resultant elimination of the posterior portion of the fronto-parietal fontanel (108).
135. The irregular patch of black pigmentation on the fourth to seventh scales of the lateral-line series and on the

third and fourth scales of the scale row immediately ventral to the lateral line (115).

136. The anteriorly undivided procumbent spine (121; optimized as a secondary reversal of the anteriorly divided procumbent spine synapomorphic for Prochilodontidae within the hypothesis of overall most parsimonious relationships herein).

No autapomorphies for *Ichthyoelephas humeralis* were identified in this study, but *I. longirostris* is defined by two autapomorphies:

137. The possession of 50 to 76 teeth in the inner tooth row on each side of the upper jaw (22).

138. The reduction in the extent of the exposure of the dorsal portion of the parietal (see discussion under "Parietal").

Ichthyoelephas humeralis has one known autapomorphy:

139. The proportionally large aperture on the lateral surface of the maxilla in the region slightly posterior of the rear of the margin of the premaxilla (see discussion under "Premaxilla").

Homoplasies

Most of the synapomorphies highlighted under "Character Description and Analysis" and "Phylogenetic Reconstruction" and in Figures 26 to 28 reflect the pronounced restructurings of various body systems associated with the unusual, highly derived, detritivorous feeding habits of adult prochilodontids. The vast majority of these modifications are unusual and typically unique for the Prochilodontidae or its components within the Characiformes; this pattern is reflected in the consequent low level of homoplasy and is indicated by the relative high consistency index for the intrafamilial phylogeny (ci=0.98).

Only one hypothesized derived feature, the presence of dark, wavy, horizontal striping on the body that is formed by concentrations of dark chromatophores along the dorsal and ventral margins of scales (Character 116), occurs homoplastically under the final phylogeny within prochilodontids, being present in a clade within *Prochilodus* (Synapomorphy 75), on the one hand, and in all species of *Semaprochilodus* (Synapomorphy 96), on the other. It should be noted, however, that the polarization of another 12 synapomorphies, approximately 10% of the total, is not based upon unequivocal hypotheses of synapomorphy based upon a priori polarization of the feature derived from outgroup information. Rather, their recognition as synapomorphies derives from homology propositions that maximize reversals relative to parallelisms (de Pinna, 1991) or is a consequence of character distribution optimization within the context of the overall most parsimonious hypothesis of intrafamilial relationships.

Two of the examined features, the degree of development of the primitively medial portion of the fourth upper pharyngeal tooth plate (Character 10) and the possession of an anteriorly divided procumbent dorsal-fin spine (Character 121), were hypothesized to have arisen at the level of the Prochilodontidae and to have been reversed in *Ichthyoelephas* in order to maximize homology propositions (reversals rather than parallelisms) following the proposal of de Pinna (1991). If we did not choose such maximization, both features could equally parsimoniously be hypothesized to have arisen independently in *Prochilodus* and *Semaprochilodus* and, as such, represent homoplasies for these two genera within the context of the final phylogeny. In addition, 10 characters for which the outgroup condition was unknown are optimized within the context of the final phylogeny as synapomorphies. These optimized synapomorphies are for *Prochilodus* (Character 6), *Semaprochilodus* (Characters 72, 81), *Ichthyoelephas* (Characters 43, 54, 97, 102), and the clade that consists of *Ichthyoelephas* plus *Semaprochilodus* (Characters 49, 99).

Turning to higher phylogenetic levels beyond the Prochilodontidae, we find that there are 12 homoplasies at different levels of inclusiveness. These involve characters present in the Prochilodontidae and Curimatidae (the first outgroup), the Prochilodontidae and Anostomidae (a component of the second outgroup), the Prochilodontidae and Chilodontidae (a component of the second outgroup), and the Prochilodontidae and more distantly related taxa within the Characiformes. In so far as the phylogenetic analysis of this study does not delve into relationships within these outgroups, those 12 homoplasies are briefly summarized herein to provide a more concise overview than is possible from the comments under the character descriptions.

In the case of the homoplasies that involve the Prochilodontidae and Curimatidae, the four features of interest are (1) the lack of an ossified first infrapharyngobranchial in *Ichthyoelephas* (Character 4) and three species of *Curimata* (*C. cisandina, C. inornata, C. roseni*), (2) the more elaborate laterosensory canal system in the sixth infraorbital in *Prochilodus* (Character 75) and *Potamorhina,* (3) the presence of a fenestra passing through the lateral ethmoid in the Prochilodontidae (Character 110) and one member of *Curimata* (*C. inornata*), and (4) the presence of a procurrent spine throughout the Prochilodontidae (Character 120) and in one species of *Cyphocharax* (*C. abramoides*). The homoplasies between these various components of the Prochilodontidae and Curimatidae lack a consistent pattern. Furthermore, the Curimatidae and its subunits are defined by an extensive series of synapomorphies (Vari, 1989a), as is the situation with the Prochilodontidae and its components. Given the preponderance of the evidence, the hypothesis of homoplasy for these characters in various components of the Prochilodontidae and Curimatidae is far more parsimonious than is an assumption of their homology and the resultant hypothesis of the nonmonophyly of these families.

Three homoplasies between components of the Prochilodontidae and Anostomidae were identified: (1) the dark caudal-fin stripes in *Semaprochilodus* (Character 119) and the genus *Lep-*

orellus; (2) the medial contact of the posterior portion of the frontals in *Ichthyoelephas* (Character 107) and a subunit of the Anostomidae; and (3) the medial contact of the parietals in *Ichthyoelephas* (Character 108) and a subunit of the Anostomidae. Although the latter two features have concordant distributions in subunits of the two families, the overwhelming evidence pertinent to the question of the monophyly of the Prochilodontidae and Anostomidae and of their higher level relationships of those families (Vari, 1983, 1989a, herein) indicate that all three of these features are homoplastic.

Also within the second outgroup, we find that the Chilodontidae shares two derived features with the Prochilodontidae: (1) the lack of a blue-staining cartilage mass in the region between the palatine and the rear of the premaxilla and palatine (Character 30); and (2) the lack of implantation of the small oral teeth on the underlying jaw bones (Character 20). Questions exist about the homology of the first of these potential homoplasies in the two families, but even if it were considered to represent a homolog, the overwhelming evidence on the monophyly of the Prochilodontidae (this paper) and Chilodontidae (Vari et al., 1995:10) and of their higher level relationships (Vari, 1983, 1989a, herein; Ortí and Meyer, 1997) indicate that both of these features are homoplastically present in the two families.

Three other homoplastic features that involve more distantly related characiform taxa and the Prochilodontidae are (1) the expanded replacement tooth trench in the dentary in the Prochilodontidae and Citharinidae (albeit much less extensive in the latter family) (Character 47), (2) the longitudinally aligned, transversely compressed, ventral extension of the mesethmoid in the Prochilodontidae and a few components of the Characidae (Character 100), and (3) the procumbent predorsal spine present in the Prochilodontidae and the subfamily Stethaprioninae of the family Characidae (Character 120). Again these are clearly homoplastic within the information of this study and the results proposed by Vari (1979), Fink and Fink (1981), and Buckup (1998).

Bauplan Shifts and Evolutionary Stasis

Figures 26 and 27 highlight one of the striking results of the phylogenetic study, the high number of synapomorphies for the Prochilodontidae identified by Vari (1983:49) and in this study (see "Monophyly of the Prochilodontidae," above) along with the numerous synapomorphies for the genera and the suprageneric component of the family identified herein (Figures 26–28). These extensive synapomorphies are all the more impressive when one considers that at least at two levels of inclusiveness, that of the Prochilodontidae and that of *Ichthyoelephas,* the morphological analysis indicates that the synapomorphies identified herein represent significant underestimates of the actual degree of morphological novelty present at those nodes.

In the case of the first of these nodes, that of the Prochilodontidae, it is clear that there are numerous details of the neurocranium (see Roberts, 1973b, figs. 2–5), soft anatomical complexes (e.g., changes of musculature associated with the pronounced restructuring of the jaws, suspensorium, and branchial apparatus), digestive (Angelescu and Gneri, 1949; Menin and Mimura, 1993), and sound production (Dorn, 1972; Schaller, 1971, 1974) systems that are potentially informative for prochilodontid monophyly. Numerous synapomorphies (58) have, however, been already identified for the family, most of which are unique to the Prochilodontidae among characiforms, and our preliminary surveys have failed to reveal variation pertinent to the lack of resolution in the hypotheses of the species-level relationships within the genera *Prochilodus* and *Semaprochilodus.* In the case of *Ichthyoelephas,* we identified numerous (32) synapomorphies for the members of the genus. The significantly restructured neurocranium characteristic of *Ichthyoelephas* is a source of numerous additional synapomorphies for that genus, as would likely be the musculature associated with the massively developed jaws and fleshy lips. The enumeration of these additional synapomorphies would unnecessarily expand the paper.

Even in the absence of the identification of additional synapomorphies at the level of the Prochilodontidae and *Ichthyoelephas,* we find that the hypotheses of the monophyly of the family and its genera (*Ichthyoelephas, Prochilodus, Semaprochilodus*), along with the hypothesis of a sister-group relationship between *Ichthyoelephas* and *Semaprochilodus,* are very robust, as illustrated by the total numbers of synapomorphies at these nodes (Figure 26) and by the limited number of identified homoplasies as indicated by the high consistency indices for almost all of the examined features (see discussion under "Homoplasies," above). In light of the cornucopia of derived features at the generic and suprageneric levels within the Prochilodontidae, the paucity of synapomorphies suitable for interpreting interspecific relationships within both *Prochilodus* and *Semaprochilodus* (Figures 27, 28) is striking (although only three interspecifically derived features were identified for *Ichthyoelephas,* that genus, with only two species, is a nonquestion in terms of interspecific relationships).

In *Semaprochilodus,* the six species of the genus are equally divided between two clades, albeit with a highly skewed distribution of identified synapomorphies. The clade formed of *S. taeniurus, S. insignis,* and *S. kneri* is defined by two synapomorphies, and the sister-species relationship within that clade between *S. insignis* and *S. kneri* is supported by two synapomorphies. In contrast, the second clade within *Semaprochilodus* is only defined by one synapomorphy, and no synapomorphies pertinent to the question of the relationships among the three contained species (*S. brama, S. laticeps, S. varii*) were identified during this study.

In the case of *Prochilodus,* the resolution of the interspecific phylogeny is even less satisfactory (only three hypothesized synapomorphies among 13 species, Figure 27). One of the identified derived features is the unusual pattern of subdivisions on the individual scales that is unique to two species among prochilodontids. The two remaining hypothesized interspecific synapomorphies for *Prochilodus* involve details of pigmentation and subdivide the remaining species into two potentially nonmonophyletic assemblages of species. The morphological similarity in examined internal systems, as indicated by the poor lack of resolution of the interspecific phylogeny, correlates with the overall lack of externally apparent variation within the genus, a problem for species differentiation discussed by Mago-Leccia (1972:35) and demonstrated to a degree in the "Key to the Species of *Prochilodus*," herein.

The numerous synapomorphies at the level of the Prochilodontidae, that of the clade formed by *Ichthyoelephas* and *Semaprochilodus*, and those for the three prochilodontid genera are paralleled by major shifts in the overall bauplans, or aspects thereof, at each of those nodes. At least for some of these nodes (that of the Prochilodontidae and that of *Ichthyoelephas*) and likely for all of them, these body plan shifts are possibly correlated with the exploitation of new food resources in so far as almost all of the modifications are directly (jaws, teeth, gill arches, and associated systems) or indirectly (changes in form of neurocranium and suspensorium) associated with feeding.

Such a shift into a new overall bauplan is most obvious at the level of the Prochilodontidae, which is characterized by a series of derived features in various body systems that are unique to that lineage among characiforms. Many of these synapomorphies for the Prochilodontidae are, in turn, further modifications of derived attributes for the clade that consists of the Curimatidae plus Prochilodontidae, the primary aufwucks/detritus/periphyton feeding clade in Neotropical freshwaters.

The method of utilization of these dietary resources by the Curimatidae and Prochilodontidae differ significantly. Members of the Curimatidae apparently scoop or pick items from the bottom with their toothless jaws (Sazima, 1986; Sazima and Caramaschi, 1989; pers. observ.), with some species in the family processing the selected food items in the buccal cavity and discarding non-target components. Species of the Prochilodontidae have a totally different feeding system wherein they apparently selectively scrape food items off typically hard, submerged surfaces (Goulding et al., 1988:61; pers. observ.), using their highly developed, evertable lips and their numerous teeth. Underwater observations of *Prochilodus lineatus* by the authors in the upper Rio Paraguay basin in Brazil have shown that the species also does scoop up the surface layer of the sand substrate and then ejects the sand, indicting that at least some prochilodontids demonstrate flexibility in feeding mechanisms. The mouth, jaw, and tooth modifications of prochilodontids that were detailed in the character descriptions and that are unique to the Prochilodontidae within the Characiformes necessitated major revamping of the structure of the jaws and associated systems relative to those typical of its sister group, the Curimatidae. Curimatids, although derived in their own right (Vari, 1983:48; 1989a:52), nonetheless retain jaws distinctly less modified relative to the morphology of more generalized basal characiforms than is the case in the Prochilodontidae in which that system is dramatically restructured.

Within the Prochilodontidae we find that each genus has, in turn, a series of modifications of what might be considered to be the basal bauplan for the family. These restructurings are particularly noteworthy in the case of *Ichthyoelephas,* in which the jaws, lips, teeth, and associated morphological systems are particularly highly modified relative to the already derived conditions characteristic of the rest of the family (see "Monophyly of *Ichthyoelephas,*" above).

As discussed above, the resolution of the interspecific phylogeny within *Prochilodus* is poor, but it nonetheless yields some interesting insights into the history of the genus. The basal assemblage of *Prochilodus* consists of *P. britskii, P. magdalenae, P. reticulatus,* and *P. vimboides*. In the absence of any synapomorphies for this group of species, or a resolution of the relationships among them, it is impossible to make exact statements on the evolution and biogeography of these taxa. Nonetheless, this group of species is informative in terms of the question of the time scale for the apparent interspecific morphological stasis within *Prochilodus*. One of the four species, *P. britskii,* is the most distinctive member of the genus (Figure 39), but the other three species retain an overall bauplan typical for *Prochilodus* species (Figures 47, 57, 59). Two of the species in this assemblage, *Prochilodus magdalenae* and *P. reticulatus,* are the only members of the genus that inhabit drainages to the west of the Andean Cordilleras, living, respectively, in the Caribbean versant rivers of northwestern Colombia and the rivers draining into the Lago Maracaibo basin of northeastern Colombia and northwestern Venezuela. *Prochilodus britskii* is apparently endemic to the upper portion of the Rio Tapajós basin. The remaining species in this basal grouping, *P. vimboides,* is known from the rivers of eastern, southeastern, and southern Brazil. Thus, this basal assemblage of prochilodontids occurs to both sides of the Andean Cordilleras and covers much of both the east to west and north to south range of *Prochilodus.* The occurrence of these typically lowland-living species on the two sides of the Andean Cordilleras and the overall morphological similarity of *Prochilodus magdalenae, P. reticulatus,* and *P. vimboides,* an overall body form that is furthermore common to almost all other species in the genus, indicate that the basic bauplan for *Prochilodus* evolved prior to the final uplift of the northern portions of the Andean Cordilleras with the closure of the Maracaibo-Falcon outlet of the Río Orinoco about eight million years ago (Lundberg et al., 1988:40, fig. 20). Indeed, it is likely that *Prochilodus* distinctly predates that final closure of the Andes, given that *P. magdalenae* inhabits rivers to the west of the main cordilleras of the northern portions of the Andes. That mountain chain was in place at an earlier time period (Late Miocene; 11.8 to 10.0 million years ago; Lundberg et al., 1998:37). In light of the overall similarity of most species of *Prochilodus,* it appears that members of the genus have demonstrated little overall morphological change over the scale of at least 8 and more likely 11.8 million years.

This conclusion of evolutionary stasis within *Prochilodus,* although not based upon fossils, is congruent with the stasis hypothesized for the characiform genus *Colossoma* (Lundberg et al., 1986), which was based upon the similarity between a fossil from the La Venta Formation (Miocene; approximately 15 million years ago) and Recent examples of that genus. It furthermore correlates with the presence in the Lago Maracaibo basin of Miocene fossils of a genus of large pimelodid catfish (*Phratocephalus*) in the Urumaco Formation that are identical to the species in the Río Orinoco and Rio Amazonas basins today (Lundberg et al., 1988). Indeed, in light of the broad distribution of the species involved in this basal grouping within *Prochilodus* (*P. britskii,* Rio Tapajós; *P. magdalenae,* northwestern Colombia; *P. reticulatus,* Lago Maracaibo basin; *P. vimboides,* eastern and southeastern Brazil), their distribution on both sides of the northern portions of the Andean Cordilleras, and the complex geomorphology of the intervening regions of South America, it is likely that *Prochilodus* predates 8.0 to 11.8 million years ago, and the time period of stasis in the basic bauplan in *Prochilodus* may be even greater.

The one notable exception to the overall morphological similarity within *Prochilodus* is *P. britskii,* a species unusual not only in terms of its external distinctiveness but in other ways. Almost all species of *Prochilodus* have wide to massive geographic distributions within major drainage systems or across one or more river basins. Furthermore, all species except *P. britskii* are known from moderate to extensive series of specimens (see "Material Examined" sections in species accounts). *Prochilodus britskii,* in contrast, is only known from a handful of specimens, which were all collected at a single location in the Rio Tapajós basin (Figure 30). The South American ichthyofauna is inadequately sampled (Vari and Malabarba, 1998:9), and samples of well-studied taxa from the Rio Tapajós basin often are sparse (e.g., *Creagrutus,* Vari and Harold, 2001:45). Nonetheless, in light of the broad distributions and migratory behaviors typical for prochilodontids, such a meager sample for a prochilodontid species, as is the case for *P. britskii,* is remarkable. Further collecting efforts are necessary to determine whether the apparently restricted distribution of *P. britskii* is merely an artifact, and whether the distinctive appearance of the species is, in some fashion, correlated with habits that are unusual relative to those of its congeners.

Family PROCHILODONTIDAE

The preceding phylogenetic analysis indicates that the three genera widely recognized in the Prochilodontidae in recent decades, *Ichthyoelephas* Posada Arango (1909) with two species, *Prochilodus* Agassiz (in Spix and Agassiz, 1829) with 13 species, and *Semaprochilodus* (Fowler, 1941) with six species, are monophyletic units. Given that conclusion and their external distinctiveness, these genera are recognized as valid herein. As documented in the preceding section, the Prochilodontidae is defined by a series of internal and external synapomorphies. The external synapomorphies that facilitate the rapid recognition of all but very small juveniles of the family are the well-developed fleshy jaws that are evertable to form an oral disk; the teeth arranged in two medially separated rows in each jaw, with the inner tooth row in the form of a varyingly obtuse V and with the outer row aligned parallel to the lip margin; the numerous teeth in each jaw with up to 200 teeth in the outer tooth row of each half of the upper jaw and lower jaw, and up to 76 teeth in the inner tooth row of the left side of the upper jaw and up to 70 teeth in the inner tooth row of the left side of the lower jaw; the mobile falciform (*Ichthyoelephas*) or spoon-shaped (*Prochilodus, Semaprochilodus*) dentition; and the first infraorbital greatly expanded, with its ventral margin and the anteroventral margin of the second infraorbital delimiting a triangular notch that borders the posterior portion of the very fleshy lips.

Other features of the family in summary are as follows. The scales of adults are either cycloid or spinoid. The median scales along the dorsal midline between the posterior of the dorsal-fin base and the adipose-fin origin either have a membranous spatulate process along the posterior margin of each scale in that series (*Ichthyoelephas, Semaprochilodus*) or lack such an elaboration and are similar in form to those of adjoining portions of the body (*Prochilodus*). The poring of the lateral line is complete in all but very small individuals, with a range of 34 to 77 pored scales throughout the family. There are 5 to 13 horizontal rows of scales between the dorsal-fin origin and the lateral line; 5 to 14 horizontal rows of scales between the pelvic-fin insertion and the lateral line; 4 to 12 horizontal rows of scales between the anal-fin origin and the lateral line; 10 to 22 median predorsal scales; 11 to 26 scales between the rear of the dorsal-fin base and the adipose-fin origin; and 13 to 27 horizontal rows of scales around the caudal peduncle.

The dorsal fin is preceded by a distinct, simple (*Ichthyoelephas*) or anteriorly bifurcate (*Prochilodus, Semaprochilodus*) procumbent spine. Fin-ray count ranges are as follows: dorsal-fin rays iii,9 to 11 (count of unbranched rays includes the procumbent spine); anal-fin rays iii,7 to 9, or ii,7 to 9; pectoral-fin rays i,12 to 18; pelvic-fin rays i,7 to 9; and principal caudal-fin rays 10/9.

Total vertebrae range from 33 to 45.

Prochilodontids are medium- to large-sized fishes with a range of maximum standard lengths among recognized examined species of approximately 240 to 460 mm SL, but with *Prochilodus lineatus* reported to reach 740 mm TL (Sverlij et al., 1993:36) and *Ichthyoelephas longirostris* to more than 800 mm TL (Patiño R., 1983:82).

Key to the Genera of the Prochilodontidae

The economic importance of the members of Prochilodontidae makes them of interest to a broad spectrum of researchers that range beyond systematists to fisheries biologists, ecologists, resource managers and others. In order to make the conclusions of this study more readily available to such researchers in various South American countries, we include parallel keys to the genera and species of prochilodontids in English and Portuguese.

1. Dorsal fin preceded by simple procumbent spine without anterior bifurcation; pored lateral-line scales 4 to 7 and scales 3 and 4 of scale row under lateral line with variably developed patch of intensely black pigmentation; 20 to 70 teeth in inner tooth row on each side of lower jaw; snout and lips proportionally very highly developed .... ***Ichthyoelephas***

   Dorsal fin preceded by anteriorly bifurcate procumbent spine; pored lateral-line scales 4 to 7 and scales 3 and 4 of scale row under lateral line without patch of intensely black pigmentation; 4 to 18 teeth in inner tooth row on each side of lower jaw; snout and lips proportionally slightly to moderately developed 2

2. Scales cycloid; scales between posterior of dorsal-fin base and adipose-fin origin with membranous spatulate process along posterior margin of each scale in that series; anal and caudal fins with dark stripes, with up to 5 stripes on anal fin and up to 14 stripes on caudal fin (stripes sometimes absent in very large individuals) .... ***Semaprochilodus***

   Scales spinoid in both juveniles and adults [Figures 24, 25], scales between posterior of dorsal-fin base and adipose-fin origin similar in form to those of adjoining regions of body, without membranous spatulate process along posterior margin of each scale in that series; anal and caudal fin without dark stripes, but with caudal-fin lobes in some species with 2 to 8 irregular vertical bars or wavy lines formed of small dark spots composed of groups of chromatophores .... ***Prochilodus***

Chave de Identificação dos Gêneros de Prochilodontidae

1. Nadadeira dorsal precedida de espinho simples, não bifurcado anteriormente; escamas perfuradas de número 4 a 7 da linha lateral e 3 e 4 da fileira imediatamente ventral com graus variáveis de pigmentação negra intensa; 20 a 70 dentes na fileira interna de cada lado da maxila inferior; focinho e lábios extremamente desenvolvidos ... . ***Ichthyolephas***

   Nadadeira dorsal precedida de espinho bifurcado anteriormente; escamas perfuradas de número 4 a 7 da linha lateral ou 3 e 4 da fileira imediatamente ventral sem pigmentação negra intensa; 4 a 18 dentes na fileira interna de cada lado da maxila inferior; lábios e focinho pouco ou moderadamente desenvolvidos, comparativamente 2

2. Escamas ciclóides; escamas entre o final da base da nadadeira dorsal e origem da adiposa com processo espatulado membranoso posterior desenvolvido; nadadeiras anal e caudal com faixas escuras; até 5 faixas na nadadeira anal e até 14 faixas na nadadeira caudal (faixas algumas vezes ausentes in indivíduos maiores) .... ***Semaprochilodus***

   Escamas ctenóides (=espinóides) em adultos e juvenis [Figuras 24, 25], escamas entre o final da base da nadadeira dorsal e origem da adiposa normais, sem processo espatulado membranoso posterior; nadadeiras anal e caudal sem faixas escuras; caudal sem manchas ou com 2 a 8 fileiras verticais irregulares e sinuosas de pequenas manchas escuras formadas por agrupamentos de cromatóforos ...... ***Prochilodus***

Genus *Ichthyoelephas* Posada Arango, 1909

Ichthyoelephas Posada Arango, 1909:300 [type species: *Ichthyoelephas pataló* Posada Arango, 1909 [=*Ichthyoelephas longirostris* (Steindachner, 1879)], by monotypy. Gender masculine.

Ichthyoëlephas.—Böhlke, 1958:109 [addition of accent to genus name].

DIAGNOSIS.—*Ichthyoelephas* is a monophyletic group delimited by the synapomorphies detailed under "Monophyly of *Ichthyoelephas*," above, and that differs from the other genera in the Prochilodontidae in the following combination of characters: dorsal fin preceded by a simple, nonbifurcated procumbent spine; snout and lips, particularly upper lip, comparatively greatly developed; teeth elongate and falciform except when worn down; 27 to 76 teeth in the internal row of each upper jaw and 20 to 70 teeth in the internal row of each lower jaw; scales cycloid, with exposed border smooth and posterior margin membranous; scales along middorsal series between posterior of dorsal-fin base and adipose-fin origin with spatulate membranous process along posterior border of each scale in that series; all fins hyaline except dorsal fin, which bears diffuse dark spots; scales 4 to 7 of lateral line series and scales 3 and 4 of scale row immediately ventral of lateral line series with irregular patches of dark pigmentation.

Ichthyoelephas species have the lateral line complete, with 36 to 40 pored scales; 6 or 7 horizontal rows of scales between the dorsal-fin origin and the lateral line; 5 or 6 horizontal rows of scales between the pelvic-fin insertion and the lateral line; 5 or 6 horizontal rows of scales between the anal-fin origin and the lateral line; 11 to 14 median predorsal scales; 11 to 14 median scales between the posterior of the dorsal-fin base and the adipose-fin origin; 15 or 16 horizontal rows of scales around the caudal peduncle; and 33 to 35 vertebrae.

REMARKS.—*Ichthyoelephas* consists of two species with notably disjunct distributions in the Pacific slope rivers of western Ecuador and the Caribbean Sea versant of northern Colombia (Figure 30). The degree of meristic, morphometric, and pigmentation variation in the genus is limited. The maximum standard lengths of the examined specimens of the two species of *Ichthyoelephas* were 239.9 (*I. humeralis*) and 431.0 mm (*I. longirostris*), but Dahl (1971:107) reported that *I. longirostris* (identified by that author as *I. longirostris longirostris*) attained lengths of greater than 500 mm SL, an observation in keeping with the results reported on by Patiño R. (1973:82) and Román-Valencia (1993b, figs. 3, 4, 8) who reported that the species grows to more than 800 mm TL.

The first description of a species now assigned to *Ichthyoelephas* was that of *Prochilodus humeralis* Günther (1859) from the Pacific Ocean versant of western Ecuador. Two decades later Steindachner (1879b) described *Prochilodus longirostris* from the Río Cauca, a tributary of the Río Magdalena that drains much of the Caribbean Sea slope of northwestern Colombia. In 1909, Posada Arango proposed *Ichthyoelephas* to include *I. pataló*, a nominal form described in the same (1909) publication. Although Posada Arango (1909:300) cited Steindachner's (1879b) *Prochilodus longirostris* in the publication in which he described *Ichthyoelephas pataló*, he presumably did not recognize the similarities of the two nominal species that are herein considered to be conspecific (see discussion under *Ichthyoelephas longirostris*).

Ridoutt (1939:69), using misidentified material, questionably equated *Prochilodus humeralis* with *Ichthyoelephas* but puzzlingly did not utilize the combination *Ichthyoelephas humeralis* in his publication. The first author to formally propose the conspecificity of *Prochilodus longirostris* and *Ichthyoelephas pataló* and to utilize the combination *Ichthyoelephas longirostris* was Miles (1943:43). In that same publication, Miles (1943:45) also suggested that *Prochilodus humeralis* Günther was closely aligned with *Ichthyoelephas longirostris*, but Miles did not shift *Prochilodus humeralis* into *Ichthyoelephas*. Böhlke (1958:112) followed up on Miles' proposal (1943) and formally recognized *Prochilodus humeralis* as *Ichthyoelephas humeralis*. The results of the phylogenetic analysis in this study indicate that the distinctive derived modifications shared by *I. longirostris* and *I. humeralis* delimit a monophyletic group, and we follow the practice advocated by Miles (1943) and Böhlke (1958) and herein recognize *Ichthyoelephas*.

Key to the Species of *Ichthyoelephas*

Snout length 34.5%–45.4% of HL; horizontal width of orbit 19.4%–36.1% of HL; 6 horizontal rows of scales between dorsal-fin origin and lateral line; 27–47 teeth in inner tooth row on each side of upper jaw .... ***I. humeralis***
(Pacific Ocean versant rivers of Ecuador)

Snout length 48.8%–55.7% of HL; horizontal width of orbit 11.1%–16.3% of HL; 7 (rarely 6) horizontal rows of scales between dorsal-fin origin and lateral line; 50–76 teeth in inner tooth row on each side of upper jaw .... ***I. longirostris***
(Ríos Cauca, Magdalena, and Rancheria, Colombia)

Chave de Identificação das Espécies de *Ichthyoelephas*

Comprimento do focinho 34.5%–45.4% do comprimento da cabeça; diâmetro horizontal do olho 19.4%–36.1% do comprimento da cabeça; 6 fileiras transversais de escamas da origem da nadadeira dorsal à linha lateral; 27–47 dentes na fileira interna de cada lado da maxila inferior .... ***I. humeralis***
(rios costeiros do Equador)

Comprimento do focinho 48.8%–55.7% do comprimento da cabeça; diâmetro horizontal do olho 11.1%–16.3% do comprimento da cabeça; 7 (raramente 6) fileiras transversais de escamas da origem da nadadeira dorsal à linha lateral; 50–76 dentes na fileira interna de cada lado da maxila inferior . . . . ***I. longirostris***
(Rios Cauca, Magdalena e Rancheria, Colômbia)

Ichthyoelephas humeralis (Günther, 1859)

FIGURES 29, 30; TABLE 3

Prochilodus humeralis Günther, 1860:419 [type locality: Western Andes of Ecuador]; 1864:294 [based upon Günther, 1959].—Eigenmann and Eigenmann, 1891:48 [in listing of South American fishes].—Boulenger, 1898:5 [Ecuador, Río Peripa].—Fowler, 1906:311 [cited as closely related to *Prochilodus steindachneri*]; 1911:497 [comparison with *Prochilodus stigmaturus*]; 1975: 359 [citation].—Eigenmann, 1907b:768 [lateral line scale count]; 1910:424 [in listing of South American fishes]; 1920b:16 [Guayaquil basin]; 1921:514 [Río Guayas basin]; 1922a:113 [western Ecuador; Bay of Guayaquil basin; common names].—Miles, 1943:45 [suggested shift from *Prochilodus* to *Ichthyoelephas*]; 1947:135 [reiteration of Miles, 1943]; 1973:42 [repeat of Miles, 1943].—[Not Ridoutt, 1939:69; Fowler, 1945:124.]

Ichthyoëlephas humeralis.—Böhlke, 1958:110 [Ecuador, Río Chimbo and Río Santiago; transfer of species from *Prochilodus* to *Ichthyoelephas*; accent added to generic name].

Ichthyoelephas humeralis.—Ovchynnyk, 1967:32 [Ecuador, western slope rivers]; 1968:251 [Ecuador, western slope rivers].—Mago-Leccia, 1972:68 [Ecuador].—Roberts, 1973a:502 [Ecuador, Río Vinces basin, Río Nuevo]; 1973b:214 [Ecuador; osteology].—Géry, 1977:226 [Ecuador].

Ichthyoelephas sp.—Vari, 1983:4; 1989:11 [in listing of anatomical material].

DIAGNOSIS.—*Ichthyoelephas humeralis* differs from its only congener, *I. longirostris,* in the snout length (34.5%–45.4% of HL versus 48.8%–55.7% of HL, respectively), the horizontal width of the orbit (17.4%–36.1% of HL versus 11.1%–16.3%, respectively), the number of horizontal rows of scales between the dorsal-fin origin and the lateral line (6 versus typically 7, rarely 6, respectively), and the number of teeth in the inner tooth row on each side of the upper jaw (27–47 versus 50–76, respectively). The proportionally large aperture on the lateral surface of the maxilla in the region slightly posterior of the rear margin of the premaxilla is an autapomorphy for *I. humeralis* (see discussions under "Maxilla" and "Character Description and Analysis," above).

DESCRIPTION.—Morphometric and meristic data for *Ichthyoelephas humeralis* presented in Table 3. Body moderately high and subcylindrical. Greatest body depth at dorsal-fin origin. Dorsal profile of head gently concave, more so anteriorly. Predorsal profile of body moderately convex; profile distinctly posteroventrally inclined along dorsal-fin base; ranging from gently convex to straight in region between posterior of dorsal-fin base and adipose-fin origin and concave along caudal peduncle. Predorsal portion of body with slightly developed median ridge. Postdorsal region of body transversely rounded. Ventral profile of body gently convex from tip of lower jaw to posterior of anal-fin base. Ventral profile of caudal peduncle concave. Prepelvic region transversely flattened proximate to pelvic-fin insertion. Region between pelvic-fin insertion and anus with poorly developed median midventral keel.

TABLE 3.—Morphometrics and meristics of *Ichthyoelephas humeralis:* (A) lectotype of *Prochilodus humeralis,* BMNH 1860.6.16:197; (B) paralectotypes of *Prochilodus humeralis,* BMNH 1860.6.16:198–199; and (C) all specimens of *Ichthyoelephas humeralis* from which counts and measurements were taken. Standard length is presented in mm; values 2 to 16 are percentages of SL, 17 to 21 are percentages of HL.

Character	A	B	C
		Morphometrics	
1. Standard length	115.1	110.0–115.9	67.6–239.9
2. Greatest body depth	35.4	32.5–34.7	29.0–38.0
3. Predorsal length	47.9	46.7–47.0	45.1–52.2
4. Dorsal-fin base length	17.3	16.0–16.5	14.6–17.3
5. Dorsal fin to adipose fin distance	26.6	27.4–27.8	24.0–28.4
6. Dorsal fin to caudal fin distance	42.2	40.9–44.1	38.9–45.2
7. Prepelvic length	54.0	52.5–54.3	49.0–57.0
8. Preanal distance	77.6	77.2–78.7	73.3–79.1
9. Snout to anal-fin insertion	81.9	81.3–83.3	78.5–83.3
10. Anal-fin base length	11.2	9.7–10.6	8.8–11.8
11. Caudal-peduncle length	11.8	12.3–13.7	10.3–14.4
12. Dorsal-fin length	29.1	26.7–27.4	25.0–31.2
13. Pectoral-fin length	22.2	20.6–21.4	18.9–22.9
14. Pelvic-fin length	20.8	18.1–19.5	17.3–20.9
15. Least caudal-peduncle height	11.9	11.0–11.1	9.8–12.1
16. Head length	28.7	27.5–28.5	26.1–31.3
17. Snout length	37.6	37.0–37.6	34.5–45.4
18. Bony orbital diameter	26.4	24.5–25.7	17.4–36.1
19. Postorbital length	40.0	40.3–40.3	36.2–44.5
20. Interorbital width	48.2	44.5–48.2	40.3–52.3
21. Mouth width	41.2	37.3–39.9	36.5–51.2
		Meristics	
Lateral-line scales	38	37–38	36–38
Scale rows between dorsal-fin origin and lateral line	6	6	6
Scale rows between anal-fin origin and lateral line	5	5–5	5–6
Scale rows between pelvic-fin insertion and lateral line	5	5–6	5–6
Rows of scales around caudal peduncle	16	16	15–16
Median predorsal scales	11	13	11–14
Median scales between dorsal and adipose fins	11	11–12	11–14
Vertebrae	33	34	33–35
Inner row teeth, upper jaw	31	29	27–47
Inner row teeth, lower jaw	27	27	20–39

Head profile blunt rounded anteriorly. Mouth subterminal. Snout length greater than horizontal width of orbit. Nares of each side of head close to each other; anterior nares circular, posterior crescent shaped. Adipose eyelid present, but poorly

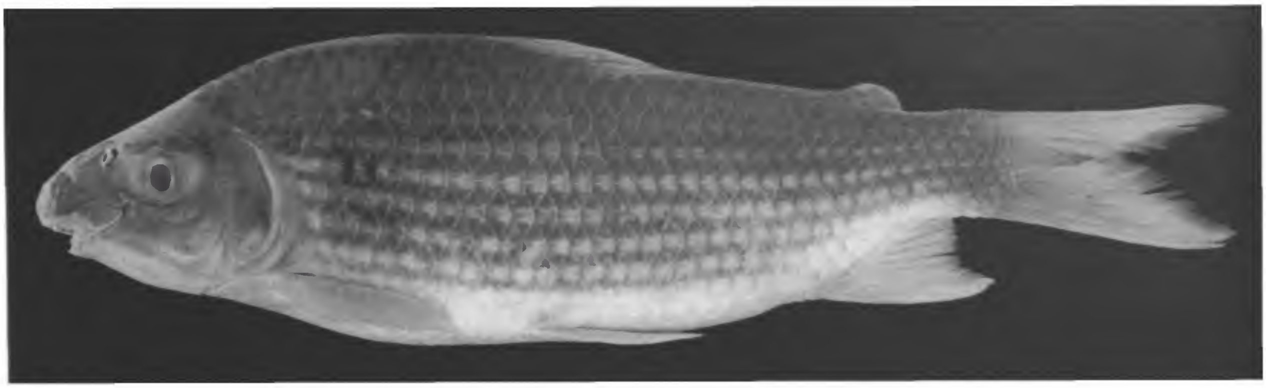


FIGURE 29.—*Ichthyoelephas humeralis*, USNM 290374, 213.7 mm SL; Ecuador, Los Ríos, Quevedo.

developed overall; more developed along anterior border of eye, but with major part of eye uncovered. Lips fleshy, highly developed, and forming oral disk when protracted.

Functional teeth in two rows in each jaw. All teeth movably implanted in flesh that overlies jaws; exposed portion of teeth falciform from anterior view. Inner tooth series with 27 to 47 teeth on left side of upper jaw and 20 to 39 teeth on left side of lower jaw. Outer row of teeth with approximately 100 teeth on each side of upper jaw and approximately 120 teeth on each side of lower jaw in lectotype. Upper and lower lips bordered by numerous fleshy transverse ridges.

Scales cycloid. Scales in middorsal series between posterior of dorsal-fin base and adipose-fin origin similar in form to those of adjoining regions of body, but with membranous spatulate process along posterior margin of each scale in that series. Series of scales that border middorsal series with less developed fleshy flaps along dorsal portions; flaps more developed in larger specimens and on scales close to dorsal fin. Lateral line with 36 to 38 (68.3% of specimens with 37) pored scales; 6 horizontal rows of scales between dorsal-fin origin and lateral line; 5 or 6 (91.7% of specimens with 5) horizontal rows of scales between pelvic-fin insertion and lateral line; 5 or 6 (95% of specimens with 5) horizontal rows of scales between anal-fin origin and lateral line; 11 to 14 (59.3% of specimens with 12) median predorsal scales; 11 to 14 (56.1% of specimens with 12) scales in middorsal series between posterior of dorsal-fin base and adipose-fin origin; 15 or 16 (98.3% of specimens with 16) horizontal rows of scales around caudal peduncle.

Vertebrae 33 to 35 (90.3% of specimens with 34).

Dorsal fin preceded by small, distinct, anteroventrally developed, nonbifurcate procumbent spine. Dorsal-fin rays (including procumbent spine) iii,9 or 10 (iii,10 most frequent) [iii,10]; anal-fin rays iii,7 to 9 (iii,8 most frequent) [iii,8]; pectoral-fin rays i,14 to 17 (i,15 most frequent) [i,16]; pelvic-fin rays i,8 or 9 (i,8 most frequent) [i,8]; principal caudal-fin rays 10/9 [10/9].

Dorsal fin truncate distally; posterior unbranched and anterior branched rays longest and subequal. Dorsal-fin origin closer to tip of snout than to caudal-fin base. Greatest length of adipose fin approximately equal to, or slightly longer than, horizontal width of orbit. Adipose-fin origin located along vertical that passes though anterior one-half of length of anal-fin base. Pectoral fin pointed distally. Tip of adpressed pectoral fin reaching posteriorly approximately two-thirds of distance between pectoral-fin and pelvic-fin insertions. Pelvic fin falcate, with origin situated slightly posterior of vertical that passes through posterior one-third of dorsal-fin base. Tip of adpressed pelvic fin extending posteriorly approximately two-thirds of distance from pelvic-fin insertion to anus. Axillary scale present, with length approximately one-third of greatest length of pelvic fin. Anal fin with straight to slightly concave distal margin, with posterior unbranched and anterior branched anal-fin rays longest and subequal. Caudal fin distinctly bifurcate.

COLORATION IN ALCOHOL.—Ground coloration silvery yellow, with dorsal portions of body and head darker. Lateral surface of body with 9 to 16 dark, irregular, vertically aligned, diffuse dark patches between head and caudal fin. Patches with approximate overall form of narrow isosceles triangles with apexes on ventrolateral portion of body and bases on dorsomedial region of body. Patches well developed in smaller specimens but indistinct or absent in larger individuals. Perforated scales 5 and 6 and sometimes also scales 4 and 7 of lateral line with irregular fields of dark pigmentation; when pigmentation limited to scales 5 and 6, then scale 5 most intensely pigmented. Scales 3 and 4 of scale row immediately ventral to lateral line with irregular fields of dark pigmentation.

Dorsal fin with 6 very irregular dark stripes and diffuse marks; marks beginning on second branched ray and extending across fin approximately parallel to base of fin. Adipose fin with dusky border. Pectoral, pelvic, anal, and caudal fins uniformly dusky. Iris reddish brown, with diffuse dusky areas on dorsal and ventral portions.

FIGURE 30.—Map of northern, central, and south central South America showing geographic distribution of *Ichthyoelephas humeralis* (diamonds; type locality inexact="Western Andes of Ecuador"), *Ichthyoelephas longirostris* (stars; 1=lectotype locality of *Prochilodus longirostris* and approximate type locality for *Ichthyoelephas pataló*), *Prochilodus argenteus* (dots; 2=neotype locality of *Prochilodus argenteus*), *Prochilodus brevis* (triangles; 3=lectotype locality of *Prochilodus brevis*; 4=lectotype locality of *Prochilodus cearensis*), and *Prochilodus britskii* (square=holotype locality) (some symbols represent more than one collecting locality and/or lot of specimens).

COLORATION IN LIFE.—(Based upon a color photograph of recently collected adult specimens from the Río Vinces, 5 km upstream of the city of Vinces, Department of Los Ríos, Ecuador, provided by Ramiro Barriga, MEPN). Dark pigmentation as described above under "Coloration in Alcohol." Ground coloration silvery golden, with dorsal portion of head and body distinctly darker. Bones of lateral surface of head with intense yellow pigmentation. Ventral region of head white. All fins yellowish, but with reddish cast to pelvic and anal fins. Iris golden brown.

DISTRIBUTION.—*Ichthyoelephas humeralis* is known from the Río Guayas, Río Chimbo, and Río Santiago basins of the Pacific Ocean versant rivers of Ecuador (Figure 30, diamonds; see also comments under "Remarks," below).

COMMON NAME.—Ratón, Guavina, and bocachico (Ecuador).

REMARKS.—*Prochilodus humeralis* was originally described by Günther (1860:419) from three specimens (BMNH 1860.6.16:197–199) collected by Fraser at an indefinite locality reported as the "Western Andes of Ecuador." Because of the range in condition of the syntypes series, we herein designate the syntype in the best condition (BMNH 1860.6.16:197, 115.1 mm SL) as the lectotype of the species, and the other syntypes (BMNH 1860.6.16:198–199, 110.0–115.9 mm SL) become paralectotypes. All examined specimens of *Ichthyoelephas humeralis* with definite locality information originated in the Pacific versant rivers of Ecuador. It is likely that the type series of the species came from that region, most likely from the Río Guayas basin, which has a major port (Guayaquil) at its mouth and which has been the source of zoological material for museums for more than a century and one-half.

The citation for *Prochilodus humeralis* for the Peruvian ichthyofauna by Fowler (1945:124) and repeated by Ortega and Vari (1986:11; as *Ichthyoelephas humeralis*) was apparently based upon the report by Ridoutt (1939:69), who cited this species from the Ríos Urubamba and Perené on the Amazonian slopes of Peru. Ridoutt (1939:69) failed, however, to explicitly state the basis for his citation of the species from Peru, and his accompanying illustration of *P. humeralis* was likely based upon the photograph of *Prochilodus humeralis* presented by Eigenmann (1922a:316, pl. 20: fig. 1). No specimens of *Ichthyoelephas* examined during this study originated in the Cis-Andean portions of South America. We consequently treat the report of *Ichthyoelephas* in eastern Peru by Ridoutt (1939:69) as erroneous and consider *I. humeralis* to be limited to the Pacific Ocean versant of Ecuador.

One specimen of *Ichthyoelephas humeralis* (ANSP 45467) has an inexactly stated locality of "Colombia," which, if correct, would represent the only non-Ecuadorian record of the species. According to the associated cataloging information, this specimen was collected by C.H. Eigenmann in 1914; however, Eigenmann (1922:13) reported that he collected in Colombia in 1912. Furthermore, in his subsequent discussion of *Prochilodus* (=*Ichthyoelephas*) *humeralis*, Eigenmann (1922:113) only cited specimens collected by Henn in 1914, which were all from the rivers draining into the "Bay of Guayaquil," southern Ecuador. These inconsistencies cast doubt on the stated locality and date of collection for ANSP 45467. Some examined *I. humeralis* specimens originated, however, in the Río Santiago basin, Esmeraldas Province, northwestern Ecuador (ANSP 75965, CAS-SU) proximate to the Ecuadorian-Colombian border. Such geographic proximity leaves open the possibility of the occurrence of *I. humeralis* in southwestern Colombia.

MATERIAL EXAMINED.—128 specimens (67, 67.6–239.9 mm SL).

ECUADOR. *Asuay:* Río Chimbo, near Bucay (latter locality at (2°41'S, 79°40'W), USNM 164031, 2 (2, 121.1–138.7). *Esmeraldas:* lower Río Santiago, near Borbón, ANSP 75965 (formerly 569–70), 2 (2, 120.3–127.1); CAS-SU 49783, 3 (3, 119.1–130.5) [3R]. *Guayas:* Naranjito, Río Barranca Alta, BMNH 1920.12.20:77–8, 2 (1, 145.3–160.8); CAS 58982 (formerly IU 13577), 11 (11, 89.9–213.3) [11R]. Colimes, Río Daule, AMNH 53557, 2 (2, 73.7–93.8); BMNH 1920.12.20:75–76, 2 (1, 74.8–80.8); CAS 58976 (formerly IU 13112), 10 (10, 67.6–142.3) [5R]; CAS-SU 22747, 4 (4, 73.6–84.2) [4R]; MCZ 48724, 4 (73.0–92.0); UMMZ 197553, 4 (1, 74.2–81.3); USNM 76961, 5 (5, 76.1–90.8). Río Chimbo, near to Bucay, ANSP 75964 (formerly 566), 1 (1, 169.4); USNM 164028, 1 (1, 191.5) [1R]. Mouth of Río Guayas, BMNH 1971.2.11:9–10, 2 (1, 170.0–239.9). Guayaquil, Río Guayas, CAS 58888, 1 (1, 234.2). Guayaquil, USNM 76960, 2 (2, 112.0–137.6). *Los Rios:* Centro Científico Río Palenque, Río Palenque, FMNH 79062, 3 (1, 198.0–221.8); FMNH 80715, 13 (1, 103.9–127.5). Quevedo fish market, MCZ 48850, 21 (2, 137.5–206.9); MZUSP 21420, 1 (150.0); USNM 290374 (originally MCZ 48850, in part), 2 (212.4–213.7; specimens cleared and counterstained for bone and cartilage. Vinces, BMNH uncatalogued, 3 (1, 145.3–152.2); CAS 58975 (formerly IU 13111), 4 (4, 140.1–159.6) [4R]. Vinces, Río Vinces (Nuevo), MCZ 48723, 1 (122.0). Río Vinces, 5 km upriver of city of Vinces, LIRP 1307, 7 (99.2–155.6); USNM 311294, 6 (97.5–157.0). Arroyo Bambine, tributary of Río Crystal, Montalvo, MCZ 48724, 2 (123.0–131.0). *Inexact Locality:* "Western Andes of Ecuador," BMNH 1860.6.16:197, 1 (1, 115.1, lectotype of *Prochilodus humeralis*) [1R]; BMNH 1860.6.16:198–199, 2 (2, 110.0–115.9, paralectotypes of *Prochilodus humeralis*) [2R]. Western Ecuador, under bridge over Río Macul, on road between Quevedo and Manta, FMNH 93138, 2 (1, 132.1–135.8). No specific locality, USNM 231437, 1 (108.5, specimen cleared and stained for bone).

COLOMBIA. *Inexact Locality* (cited locality perhaps erroneous; see comments under "Remarks," above): ANSP 45467, 1 (1, 86.9).

Ichthyoelephas longirostris (Steindachner, 1879)

FIGURES 30, 31; TABLE 4

Prochilodus longirostris Steindachner, 1879b:195 [type locality: Cauca (=Río Cauca, Colombia), restricted herein to Colombia, Antióquia, Río Cauca, near to Cáceres; brief abstract of more extensive species description published in Steindachner, 1879c]; 1879c:188 (page 70 of separate) [more extensive description of species]; 1880:69 [Colombia: Río Cauca; expanded species description].—Eigenmann and Eigenmann, 1891:48 [in listing of South American fishes].—Eigenmann, 1907b:768 [lateral-line scale count]; 1910:424 [in listing of South American fishes]; 1920b:16 [(Río) Magdalena basin]; 1922a:112 [Cauca; based upon Steindachner, 1879c].—Posada Arango, 1909:300 [Cauca].—Ridoutt, 1939:69 [in key to species of *Prochilodus*].—Fowler, 1942:133 [Colombia, Ríos Magdalena and Cauca].—Böhlke, 1958: 112 [features shared with *Ichthyoelephas humeralis* noted].—[Not Magalhães, 1931:239.]

Ichthyoelephas pataló Posada Arango, 1909:302, fig. on page 301 [type locality: Colombia, Samana (=Río Samaná)].

Ichthyoelephas longirostris.—Miles, 1943:43 [Colombia, Río Cauca basin; shift of species from *Prochilodus* to *Ichthyoelephas*; repeat of original description of species; illustration of external head osteology]; 1947:133 [Colombia, Río Magdalena basin, upper Río Cauca basin]; 1973:39 [repeat of account in Miles, 1943].—Mago-Leccia, 1972:68 [Colombia].—Roberts, 1973b:214, fig. 1 [Colombia].—Patiño R., 1973:81, fig. 29 [Colombia, Río Cauca basin, distribution, life history, anthropogenic effects on populations].—Fowler, 1975:357 [literature compilation].—Géry, 1977:226, unnumbered figure on page 222 [Colombia].—Román-Valencia, 1988:111 [Colombia, Departamento de Quindio, upper Río Cauca]; 1993:71 [life history; Colombia, upper Río Cauca basin, Río La Vieja].—Cala, 1995:49 [Colombia, Río Magdalena basin, Betania Reservoir; reductions of populations in and upriver of that impoundment].—Mojica-C., 1999:554 [Colombia, Río Magdalena, Río Cesar, Río San Jorge, upper Río Cauca].—Sánchez, M. et al., 2000:218 [Colombia, Departamento del Huila, upper Río Magdalena; economic importance].—Román-Valencia and Ortiz-Muñoz, 2001:33 [Colombia: Río Magdalena-Cauca basin, Río Rancheria (state of Guajira); reproduction].

Ichthyoëlephas longirostris.—Dahl et al., 1963:43 [Colombia, Río San Jorge; habitat preferences; common name].—Román-Valencia, 1995, unpaginated [Colombia, upper Río Cauca basin, Río La Vieja; details of life history].

Ichthyoelephas longirostris longirostris.—Dahl, 1971:107 [Colombia, upper portions of Rio Magdalena basin and its tributaries; food habits, economic importance].

Ichthyoelephas longirostris neglectus Dahl, 1971:108 [type locality: Colombia, ciertas ciénegas adyacentes al Bajo Río Magdalena, desde la Ciénega de Plata hacia abajo (=certain "ciénegas" (floodplain pools and swamps) adjacent to lower Río Magdalena, from Ciénega de Plato downriver); common name].—Román-Valencia, 1993b:78 [as synonym of *Ichthyoelephas longirostris*].

DIAGNOSIS.—*Ichthyoelephas longirostris* differs from the only other member of the genus, *I. humeralis*, in the snout length (48.8%–55.7% of HL versus 34.5%–45.4% of HL, respectively), the horizontal width of the orbit (11.1%–16.3% versus 19.4%–36.1% of HL, respectively), the number of horizontal rows of scales between the dorsal-fin origin and the lateral line (typically 7, rarely 6, versus 6, respectively), and the number of teeth in the inner row of teeth on each side of the upper jaw (50 to 76 versus 27 to 47, respectively). The latter feature is an autapomorphy for *I. longirostris*, along with the reduction in the extent of the exposure of the parietal on the dorsal surface of the neurocranium (see "Parietal" under "Character Description and Analysis").

DESCRIPTION.—Morphometric and meristic data for *Ichthyoelephas longirostris* presented in Table 4. Body moderately high, typically subcylindrical, but relatively deeper in some larger, apparently female specimens. Greatest body depth at dorsal-fin origin in most specimens, but slightlyanterior to that point in some smaller individuals. Dorsal profile of head very gently convex. Predorsal profile of body moderately convex. Dorsal profile of body posteroventrally inclined along dorsal-fin base; gently convex from posterior of dorsal-fin base to adipose-fin origin, and concave along caudal peduncle. Predorsal portion of body with slight median ridge. Postdorsal region of body transversely obtusely rounded. Ventral profile of body gently convex from tip of lower jaw to posterior of anal-fin base. Ventral profile of caudal peduncle concave. Prepelvic region transversely flattened from slightly posterior of vertical through pectoral-fin insertion to proximate to pelvic-fin insertion, more distinctly flattened posteriorly. Region between pelvic-fin insertion and anus transversely rounded and without distinct median keel.

TABLE 4.—Morphometrics and meristics of *Ichthyoelephas longirostris:* (A) lectotype of *Prochilodus longirostris*, NMW; (B) paralectotypes of *Prochilodus longirostris*, NMW 56681 and NMW 56682:1–2; and (C) all specimens of *Ichthyoelephas longirostris* from which counts and measurements were taken. Standard length is presented in mm; values 2 to 16 are percentages of SL, 17 to 21 are percentages of HL.

Character	A	B	C
		Morphometrics	
1. Standard length	366.3	306.5–390.9	232.9–431.0
2. Greatest body depth	28.2	27.3–28.5	27.1–33.0
3. Predorsal length	43.5	43.7–46.2	42.8–49.3
4. Dorsal-fin base length	14.3	14.3–16.0	14.2–16.2
5. Dorsal fin to adipose fin distance	29.0	26.0–28.9	25.9–29.0
6. Dorsal fin to caudal fin distance	44.6	44.0–46.0	44.0–47.8
7. Prepelvic length	52.7	50.9–53.2	48.6–53.4
8. Preanal distance	76.8	74.4–78.1	71.2–78.3
9. Snout to anal fin insertion	80.3	76.7–81.1	74.5–81.2
10. Anal-fin base length	9.6	8.7–9.6	8.6–9.6
11. Caudal-peduncle length	15.6	14.9–15.7	13.9–16.0
12. Dorsal-fin length	20.9	21.0–22.9	20.0–23.2
13. Pectoral-fin length	21.3	20.7–23.8	20.7–23.8
14. Pelvic-fin length	18.2	17.7–19.4	17.5–19.5
15. Least caudal-peduncle height	12.2	11.5–11.7	11.2–14.4
16. Head length	26.6	26.1–26.5	23.5–26.6
17. Snout length	52.6	52.4–55.7	48.8–55.7
18. Bony orbital diameter	12.3	12.8–13.6	11.1–16.3
19. Postorbital length	39.7	36.0–39.2	36.0–40.9
20. Interorbital width	49.2	45.0–47.7	45.0–52.6
21. Mouth width	46.1	42.1–43.6	42.1–49.8
		Meristics	
Lateral-line scales	39	38–39	38–40
Scale rows between dorsal-fin origin and lateral line	7	7	6–7*
Scale rows between anal-fin origin and lateral line	6	5	5–6
Scale rows between pelvic-fin insertion and lateral line	6	5	5–6
Rows of scales around caudal peduncle	16	15–16	15–16
Median predorsal scales	14	13	13–14
Median scales between dorsal and adipose fins	14	12–14	12–14
Vertebrae	35	35	33–35
Inner row teeth, upper jaw	75	68–74	50–76
Inner row teeth, lower jw	68	54–60	35–70

* 6 scales only in 2 of 14 examined specimens.

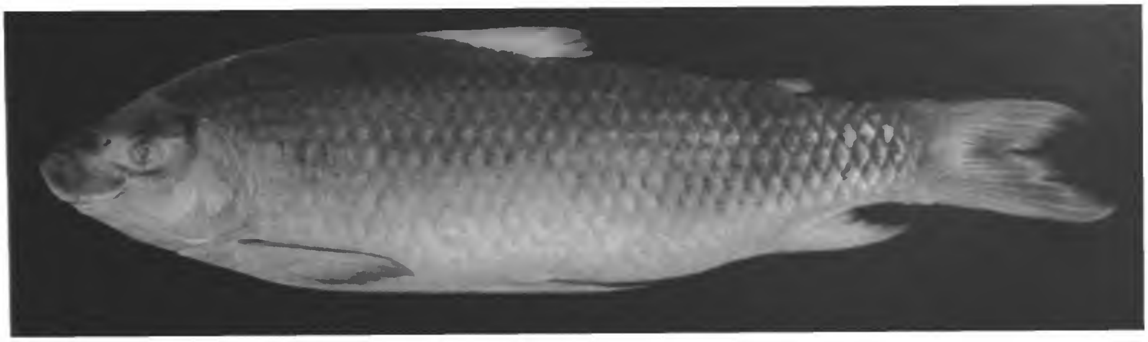


FIGURE 31.—*Ichthyoelephas longirostris*, MZUSP 55145, 325.3 mm SL; Colombia, Valle, laguna de Sonso, Río Cauca system.

Head profile pointed. Mouth subterminal and very broad. Snout length distinctly greater than horizontal width of orbit. Nares of each side of head close to each other; anterior nares circular, posterior crescent shaped. Adipose eyelid present but poorly developed; most highly developed along anterior border but with most of eye uncovered. Lips forming oral disk when protracted.

Functional teeth in two rows in each jaw. All teeth falciform and movably implanted in flesh that overlies jaws. Inner tooth series in each jaw with 50 to 76 teeth on left side of upper jaw and 35 to 70 teeth on left side of lower jaw. Outer row of teeth with approximately 200 teeth on each side of upper jaw and approximately 200 teeth on each side of lower jaw in lectotype. Upper and lower lips bordered by numerous transverse fleshy ridges.

Scales cycloid. Scales along middorsal series between posterior of dorsal-fin base and adipose-fin origin with spatulate membranous process along posterior border of each scale in that series. Lateral line with 38 to 40 (45.0% of specimens with either 38 or 39) pored scales; 6 or 7 (86% of specimens with 7) horizontal rows of scales between dorsal-fin origin and lateral line; 5 or 6 (71.5% of specimens with 5) horizontal rows of scales between pelvic-fin insertion and lateral line; 5 or 6 (78.6% of specimens with 5) horizontal rows of scales between anal-fin origin and lateral line; 13 or 14 (78.6% of specimens with 13) median predorsal scales; 12 to 14 (50% of specimens with 14) scales in middorsal series between posterior of dorsal-fin base and adipose-fin origin; 15 or 16 (78.6% of specimens with 16) horizontal rows of scales around caudal peduncle.

Vertebrae 33 to 35 (83.3% of specimens with 35).

Dorsal fin preceded by small, nonbifurcate procumbent spine. Dorsal-fin rays (including procumbent spine) iii,10 [iii,10]; anal-fin rays iii,7 or 8 (iii,8 most frequent) [iii,8]; pectoral-fin rays i,15 or 16 (i,16 most frequent) [i,16]; pelvic-fin rays i,8 [i,8]; principal caudal-fin rays 10/9 [10/9].

Dorsal fin truncate distally; posterior unbranched and anterior branched rays longest and subequal. Dorsal-fin origin located closer to tip of snout than to caudal-fin base. Greatest length of adipose fin approximately equal to distance slightly greater than horizontal width of orbit. Adipose-fin origin located along vertical that passes though posterior one-half of anal-fin base. Pectoral fin distally pointed. Tip of adpressed pectoral fin reaching approximately two-thirds of distance between pectoral- and pelvic-fin insertions. Pelvic fin falcate or with distal margin straight. Pelvic-fin origin located slightly posterior of vertical that passes through posterior one-third of dorsal-fin base. Tip of adpressed pelvic fin reaching approximately two-thirds to three-fourths of distance from pelvic-fin insertion to anus. Axillary scale present, length approximately one-third that of pelvic fin. Posterior unbranched and anterior branched anal-fin rays longest and subequal. Caudal fin distinctly bifurcate.

COLORATION IN ALCOHOL.—Ground coloration yellowish or light brown, with dorsal portion of head and body darker. Scales 4 through 6 of lateral line series with irregular patches of dark pigmentation in more recently collected specimens, with pigmentation on scale 5 most intense; dark pigmentation not apparent in some nontype specimens (NRM 24960). Scales 3 and 4 of horizontal scale row immediately ventral of lateral line series slightly pigmented with dark chromatophores in relatively recently collected, large specimens; pigmentation only apparent in some specimens in NRM 24960 collected more than 60 years ago.

Dorsal fin with 5 very irregular stripes beginning at rear of fifth branched ray and extending posteriorly across fin approximately parallel to base of fin. Adipose-fin margin outlined by dark pigmentation. Pectoral, pelvic, and anal fins dusky. Median caudal-fin rays darker than rest of fin. Iris brownish red, with diffuse dark areas dorsally and ventrally.

COLORATION IN LIFE (based upon description by Román-Valencia (1993b:78)).—Body dark green dorsally and golden white ventrally, with a dark blue band along the side of the body over yellow marks. Dorsal fin yellow-green, with dark band at base. Anal, pectoral, pelvic, and adipose fins reddish. Caudal fin dark green except for reddish band distally.

DISTRIBUTION.—Examined samples of *Ichthyoelephas longirostris* originated in the Río Cauca-Río Magdalena drainage basin of northern Colombia (Figure 30, stars). Patiño R. (1973:81) reports the species from the Río Timba, Río Rio-Claro, Río Jamundi, Río Piedras, and some tributaries to the Río La Vieja. all in the Río Cauca-Río Magdalena basin. Román-Valencia and Ortiz-Muñoz (2001:35) reported that *I. longirostris* occurs in the Río Rancheria, an independent coastal drainage in the state of Guajira, on the Peninsula of Guajira (approximately 11°34′N, 72°54′W), Colombia. This is the first record of *Ichthyoelephas longirostris* from outside of the Río Cauca-Río Magdalena drainage basin.

COMMON NAME.—Pataló, getudo, hocicón, jetón, moreno, besote, and besugo (Colombia).

LIFE HISTORY AND ECOLOGY.—Patiño R. (1973:81–82) reported that *Ichthyoelephas longirostris* reaches 80 cm (presumably TL) and that some individuals achieve even larger sizes. The species feeds on the algal covering that grows on rocks in clear-water rivers. As a consequence of their dependence upon that food source, populations of *I. longirostris* have been adversely effected by the siltation that is a consequence of the increased erosion brought about by deforestation. The ready visibility of *I. longirostris* in clear waters and market demand because of their fine taste has led to intense fishing pressure and destructive fishing methods, including the use of dynamite. This in turn has resulted in the elimination of populations of *I. longirostris* in some areas (Dahl, 1971:107). Sánchez et al. (2000:218–219) reported that the species is of commercial importance in the upper Río Magdalena basin below the Betania impoundment, being one of the most expensive fishes in the markets of the region. According to Patiño R. (1973:81–82), *I. longirostris* reproduces in running waters, with the migrating schools using leaps to overcome obstacles to their migration. Details of its life history have been discussed by Román-Valencia (1993:71) and Román-Valencia and Ortiz-Muñoz (2001:33), who provided additional information on its reproduction and habitat.

REMARKS.—Steindachner (1879b:195) described *Prochilodus longirostris* from four specimens of variable condition collected by Grosskopf in the Río Cauca, Colombia, close to Cáceres. We herein designate a ripe female (NMW 56680, 366.3 mm SL), with the abdominal cavity mostly full of yellow eggs of approximately 0.8 mm diameter and that is in the best overall condition, as the lectotype of the species. The three remaining syntypes (NMW 56681, 306.5 mm SL; NMW 56682:1-2, 381.1–390.9 mm SL) consequently become paralectotypes.

Posada Arango (1909:300) proposed *Ichthyoelephas* to contain *I. pataló*, described in the same paper. The species was based upon specimens that originated in the Río Samaná, a tributary of the Río Magdalena drainage system in northwestern Colombia. Despite the apparent absence of extant type specimens for the species (Eschmeyer et al., in Eschmeyer, 1998:1297), the examination of specimens from the approximate type locality for the species (CAS 150411, CAS 150412) and the information in the original description of *I. pataló*, in particular Posada Arango's comment that the snout is more highly developed in *I. pataló* than it is in the species of *Prochilodus*, leave no doubt that *I. pataló* is conspecific with, and a junior synonym of, *Prochilodus longirostris*, the *Ichthyoelephas longirostris* of this study.

Miles (1943:43–45) emphasized that *Prochilodus longirostris* could be distinguished from the other species assigned at that time to *Prochilodus* in various details, most notably in its cycloid scales, which differed from what he characterized as the ctenoid scales of *Prochilodus* (the spinoid scales of this study; see "Methods and Materials"), and in having a simple procumbent spine anterior to the dorsal fin rather than the anteriorly bifurcate procumbent spine typical of *Prochilodus* (the concept of *Prochilodus* used by Miles also included *Semaprochilodus* of this paper). In light of those differences, Miles (1943) shifted *Prochilodus longirostris* to *Ichthyoelephas*, an action congruent with the phylogenetic conclusions of this study.

Dahl's (1971:108–109) proposal of a new subspecies, *Ichthyoelephas longirostris neglectus*, was based upon three specimens (holotype, 172.0 mm SL, and 2 paratypes, 210.0–213.0 mm SL) that originated in ciénegas (floodplain pools and marshes) adjacent to the lower Río Magdalena, Colombia. The differences cited by Dahl to distinguish his nominal subspecies from what he recognized as *Ichthyoelephas longirostris longirostris* involved primarily the numbers of lateral-line scales and anal-fin rays, and the relative predorsal length of the body. Unfortunately, Dahl did not illustrate his new form, and the type series of that subspecies does not appear to be extant (Cala, 1981:1–3); these factors complicate the evaluation of the validity of this taxon. Román-Valencia (1993b:78) considered the two nominal subspecies recognized by Dahl (1971) to be equivalent and placed the subspecies proposed by Dahl into synonymy with *Ichthyoelephas longirostris*, albeit without an examination of the type series of the latter species. The data provided by Román-Valencia along with the information from the type series of *Prochilodus longirostris* (Table 4) indicate that populations from the Río Cauca basin have a range of lateral line counts (34 to 40) that overlap the values cited by Dahl (36 or 37) for *Ichthyoelephas longirostris neglectus* from the lower Río Magdalena. Similarly, the count of branched anal-fin rays (7 or 8) in the specimens examined in this study and by Román-Valencia for specimens from the Río Cauca system, the type region of *Prochilodus longirostris*, do not differ from those reported by Dahl for *Ichthyoelephas longirostris neglectus*.

In his description of *Ichthyoelephas longirostris neglectus*, Dahl (1971:109) differentiated that subspecies from *I. longirostris longirostris* by its proportionally shorter predorsal length. That measurement, however, is a function of the length of the fleshy snout, a feature whose form and relative dimensions in prochilodontids are functions of the state and position of the lips at the time of fixation of the specimen. This correlation is particularly problematic in the case of *Ichthyoelephas longirostris,* which has the most highly developed, fleshy upper lips in the Prochilodontidae. The preservation-induced variation in lip form in *Ichthyoelephas* species renders any measurement that is dependent, even in part, upon relative snout length highly suspect as an indicator of such subtle morphological differences as proposed by Dahl (1971) to delimit subspecies within *I. longirostris*. Another relevant consideration is the fact that many prochilodontid species (see "Remarks" under *Prochilodus nigricans*) demonstrate notable degrees of ecophenotypic variation, often of a scale greater than that purported to distinguish these nominal forms. Finally, *Ichthyoelephas longirostris* undergoes the migrations typical of other prochilodontids and is noted for its ability to overcome the barriers and obstacles that it encounters during migration (Patiño, 1973:82). Such extensive migrations make it highly unlikely that a population could significantly differentiate and remain distinct from other populations, particularly in the relatively small Río Magdalena system, which lacks significant natural intemal barriers to fish migrations. In light of all of the above factors, we agree with Román-Valencia (1993b:78) and herein consider *I. longirostris neglectus* to be a junior synonym of *I. longirostris*.

Mago-Leccia (1972:69) followed by Géry (1977:226), neither of whom apparently had examined material of *Ichthyoelephas longirostris,* proposed that this species lacked the black pigmentation on scales 5 though 7 of the lateral line series that is present in *I. humeralis* (the humeral spot of Géry (1977: 226)). In actuality, recently collected specimens of *I. longirostris* have distinct, dark pigmentation on scales 4 to 6 of the lateral line series and on the scales immediately ventral of those, and such dark coloration, albeit faint, also is still apparent in the lectotype of the species (NMW 56680). That pigmentation also is apparent in some examined specimens of the species collected many decades ago. Some specimens of *I. longirostris,* however, completely lack any dark pigmentation, most likely a consequence of their length of time in preservative or the original method of preservation. Although the purported differences in pigmentation on the anterior portion of the lateral line and proximate scales do not serve to distinguish the two species of *Ichthyoelephas,* these species unequivocally differ in various other characters (see "Diagnosis," above).

MATERIAL EXAMINED.—14 specimens (14, 232.9–431.0 mm SL).

COLOMBIA. *Antióquia:* Río Cauca, near to Cáceres, NMW 56680, 1 (366.3, lectotype of *Ichthyoelephas longirostris*) [1R]; NMW 56681, 1 (306.5, paralectotype of *Ichthyoelephas longirostris*) [1R], NMW 56682:1-2, 2 (2, 381.1–390.9, paralectotypes of *Ichthyoelephas longirostris*) [1R]. *Caldas:* At or near junction of Rios Samaná [and] La Miel, near La Dorada (5°29′N, 74°40′W), CAS 150411, 1 (431.0, formerly SU 50411); CAS 150412, 1 (335.2, formerly SU 50412). *Cauca:* Río Cauca basin (3°07′N, 76°37′W), Timba, 1100 m asl, NRM 24960, 5 (5, 232.9–263.1), NRM 24966, 1 (259.9). *Valle:* Laguna de Sonso, near to Instituto de Piscicultura Tropical de Buga, Município de Buga, valley of Río Cauca, MZUSP 55145, 2 (2, 311.2–325.3; 1 specimen cleared and counterstained for bone and cartilage) [2R].

Genus *Prochilodus* Agassiz, 1829

Prochilodus Agassiz in Spix and Agassiz, 1829:62 [type species: *Prochilodus argenteus* Agassiz in Spix and Agassiz, 1829, by subsequent designation (Eigenmann, 1910:424)]. Gender masculine.

Pacu Agassiz in Spix and Agassiz, 1829:62 [type species: *Prochilodus argenteus* Agassiz in Spix and Agassiz, 1829, by subsequent designation (Eigenmann, 1910:424)]. Gender masculine.

Paca.—Valenciennes, 1836, no page, pl. 8: fig. 3 [misspelling of *Pacu* Agassiz in Spix and Agassiz, 1829].

Chilomyzon Fowler, 1906:309 [type species: *Prochilodus steindachneri* Fowler, 1906 (=*Prochilodus vimboides* Kner, 1859), by monotypy. Proposed as a subgenus of *Prochilodus* Agassiz in Spix and Agassiz, 1829]. Gender masculine.

Pacus.—Fowler, 1941:168 [incorrect spelling of *Pacu* Agassiz in Spix and Agassiz, 1829].

DIAGNOSIS.—*Prochilodus* is a monophyletic group of 13 species delimited by the characters discussed in the "Monophyly of *Prochilodus,*" above. *Prochilodus,* furthermore, differs from *Ichthyoelephas* and *Semaprochilodus,* the other genera in the Prochilodontidae, in the following combination of characters: the dorsal fin is preceded by an anteroventrally branched procumbent spine; the fleshy lips are moderately developed; the teeth are short and spatulate from anterior view; there are 10 to 29 teeth on each side of the inner tooth row of the upper jaw and 6 to 18 teeth on each side of the inner tooth row of the lower jaw; the scales are spinoid (ctenoid of most previous authors; see "Methods and Materials") with small, flat spines in two approximately alternating rows along the posterior exposed margin; the scales in the middorsal series between the posterior of the dorsal-fin base and the adipose-fin origin are similar in form to those of adjoining portions of the body and lack a membranous spatulate process along their posterior margin.

In addition, *Prochilodus* species have the dorsal fin truncate, either rounded or slightly pointed distally; the anal fin gently falcate; the caudal fin bifurcate or gently emarginate; a dorsal fin with 2 to 10 irregular dark stripes that begin along its anterior margin and extend across the fin approximately parallel to the fin base. The pectoral, pelvic, and anal fins are hyaline; the caudal fin is hyaline or with 2 to 8 irregular, wavy, vertical bars formed of small dark marks; juveniles and smaller specimens have 4 to 24 vertical pigmentation patches on the body formed by fields of dark chromatophores with patches having an overall form of narrow isosceles triangles with apexes located on the middle of the ventrolateral portion of the body and bases on the dorsomedial region of the body.

Prochilodus species as a group have 34 to 64 pored scales; 5 to 13 horizontal rows of scales between the dorsal-fin origin and the lateral line; 5 to 11 horizontal rows of scales between the pelvic-fin insertion and the lateral line; 4 to 9 horizontal rows of scales between the anal-fin origin and the lateral line; 11 to 22 median predorsal scales; 11 to 23 scales in the middorsal series between the posterior of the dorsal-fin base and the adipose-fin origin; 13 to 25 horizontal rows of scales around the caudal peduncle; and 36 to 45 vertebrae.

REMARKS.—*Prochilodus* is the most speciose genus in the Prochilodontidae and is broadly distributed across much of South America with the notable exception of the Cis-Andean Carribean Sea versant rivers of northern Venezuela, the rivers of eastern Uruguay, the rivers of Argentina south of the La Plata region, and the Pacific Ocean versant rivers of the continent (Figures 30, 43, 52). Many of the gaps in the known distribution of the genus across the remainder of the continent are likely a consequence of the less than adequate collecting efforts across major regions of South America, as is the situation with many groups of Neotropical fishes (Vari and Malabarba, 1998:9). The distribution of *Prochilodus* and the Prochilodontidae are almost equivalent, with the exception of the various Pacific Ocean versant rivers of Ecuador that are inhabited by *Ichthyoelephas humeralis* but that lie outside the range of all *Prochilodus* species. The maximum sizes of examined specimens of the recognized species of *Prochilodus* ranges from 238.5 to 460.2 mm SL. *Prochilodus lineatus* reaches 74 cm TL (Sverlij et al., 1993:36)—a length significantly greater than that occurring in the specimens examined in this study.

The generic-level synonymy of *Prochilodus* is unusually simple for a major group of economically important Neotropical characiforms. This atypical situation perhaps reflects the relative homogeneity in meristic, morphometric, and pigmentary features within *Prochilodus*. Although some species of *Prochilodus* were originally described in other generic combinations, these are, with one exception, either typographic errors or unjustified emendations of junior synonyms of *Prochilodus* (see generic synonymy, above). The sole exception is *Chilomyzon*, proposed as a subgenus of *Prochilodus* by Fowler (1906) for *P. steindachneri* on the basis of what that author perceived to be the unusually large (i.e., relatively few) scales present in that species. *Prochilodus steindachneri*, the type species of *Chilomyzon* by monotypy, is, however, a junior synonym of *P. vimboides* Kner, 1859, a species retained by default by Fowler in *Prochilodus*. Fowler was the only author to utilize *Chilomyzon* subsequent to his proposal of the subgenus. Such an almost universal avoidance of the use of *Chilomyzon* presumably was a consequence of Eigenmann's (1907b:767–772) pointed criticism of myriad details of Fowler's 1906 publication. In particular, Eigenmann observed that the number of lateral line scales, the feature used by Fowler (1906) to distinguish *Chilomyzon* from the nominate subgenus *Prochilodus*, was actually continuous between the two subgenera; thus, the feature failed to differentiate the two subgenera. Eigenmann's observation was confirmed by this study. We consequently follow recent practice and recognize only a single genus for this assemblage of 13 species.

Key to the Species of *Prochilodus*

1. Caudal fin with 2 to 8 irregular, vertical, wavy bars formed of small black marks, but with pigmentation occasionally absent in *P. brevis;* see comments under that species (Río Orinoco, Río Amazonas, coastal rivers of the Guianas, coastal rivers of northeastern Brazil between São Luís and Salvador, including northern tributaries of lower portions of Rio São Francisco) 2

   Caudal fin hyaline (rivers of northern Colombia, Lago Maracaibo basin, Rio São Francisco, coastal rivers of Brazil between Rio Pardo, Bahia, and Rio Paraíba do Sul, Rio de Janeiro, Rio Apiacá in Rio Juruena basin, Río de La Plata basin) ... 6

2. Lateral line with 52 to 64 scales (52 scales in only one specimen) .... ***P. mariae*** (Río Orinoco basin)

   Lateral line with 41 to 52 scales (52 scales in only two specimens) (Río Caroni, Rio Amazonas, coastal rivers of the Guianas, coastal rivers of northeastern Brazil between São Luís and Salvador, including northern tributaries of lower portions of Rio São Francisco) 3

3. Scales on body with cruciform pattern of radial subdivisions, typically one extending dorsally and another ventrally and sometimes one anteriorly and posteriorly, but without complex pattern of secondary subdivisions [Figure 24] (coastal rivers of northeastern Brazil, including northern tributaries of lower portions of Rio São Francisco) 4

   Scales on body with complex pattern of secondary subdivisions in addition to regular pattern of radial lines; complex pattern not present on all scales and more frequent in larger individuals [Figure 25] (basins of Rios Amazonas, Tocantins, Branco and Marauiá, Río Caroni, and coastal rivers of Guianas) 5

4. Lateral-line scales 41 to 48 (43 most frequent, 46 to 48 infrequent) [Figure 37]; number of horizontal rows of scales between pelvic-fin insertion and lateral line 6 to 8 (7 most frequent, 8 infrequent) [Figure 37] . . . . ***P. brevis***
(small to medium-sized coastal rivers of northeastern Brazil, including northern tributaries of lower portions of Rio São Francisco)

Lateral-line scales 46 to 51 (47 most frequent) [Figure 37]; number of horizontal rows of scales between pelvic-fin insertion and lateral line 8 to 11 (9 most frequent, 8 infrequent) [Figure 37] . . . . ***P. lacustris***
(Rios Parnaíba and Mearim of NE Brazil)

5. Horizontal rows of scales around caudal peduncle 17 to 21 (19 most frequent, 17 and 18 infrequent) [Figure 54]; horizontal rows of scales between the pelvic-fin insertion and lateral line 7 to 9 (8 most frequent) [Figure 55] . . . . ***P. nigricans***
(Rio Amazonas and Rio Tocantins basins)

Horizontal rows of scales around caudal peduncle 14 to 18 (16 most frequent) [Figure 54]; horizontal rows of scales between pelvic-fin insertion and lateral line 6 or 7 (6 most frequent) [Figure 55] . . . . ***P. rubrotaeniatus***
(basins of Rios Branco and Marauiá, Río Caroni, and coastal rivers of Guianas)

6. Scales in lateral line 34 to 39 . . . . ***P. vimboides***
(coastal rivers of eastern Brazil between Rios Jucurucu and Paraíba; headwaters of upper Rios Paraná and São Francisco)

Scales in lateral line 40 to 51 (Rio Apiacá in Río Juruena basin, rivers of northern Colombia, Lago Maracaibo basin, Rio São Francisco, Rios Pardo and Jequitinhonha, Bahia, Río de La Plata basin) 7

7. Teeth in inner tooth row on each side of lower jaw 6 or 7; least height of caudal peduncle 8.8%–9.4% of SL . . . . ***P. britskii***
(Rio Apiacá in Rio Juruena basin)

Teeth in inner tooth row on each side of lower jaw 8 to 18; least height of caudal peduncle more than 9.5% of SL (rivers of northern Colombia, Lago Maracaibo basin, Rio São Francisco, Rios Pardo and Jequitinhonha, Bahia, Río de La Plata basin) 8

8. 14 to 16 horizontal rows of scales around caudal peduncle; scales in lateral line 40 to 43; 13 to 18 teeth on inner tooth row on each side of lower jaw . . . . ***P. hartii***
(Rios Pardo and Jequitinhonha basins, NE Brazil)

16 to 22 horizontal rows of scales around caudal peduncle; scales in lateral line 41 to 51; 8 to 18 teeth on inner tooth row on each side of lower jaw (rivers of northern Colombia, Lago Maracaibo basin, Rio São Francisco, Río de La Plata basin) . . . 9

9. Scales in lateral line 41 to 45 (43 most frequent); 11 to 18 median predorsal scales (13 most frequent); 38 to 40 vertebrae (39 most frequent) . . . . ***P. reticulatus***
(Lago Maracaibo basin)

Scales in lateral line 43 to 51 (44 to 48 most frequent); 12 to 22 median predorsal scales (15 to 18 most frequent); 39 to 44 vertebrae (41 to 43 most frequent) (rivers of northern Colombia, Río de La Plata basin, and Rio São Francisco) 10

10. Body without series of dark, wavy, horizontal stripes; scales in lateral line 43 to 46 (44 most frequent); 12 to 17 median predorsal scales (15 most frequent); 39 to 41 vertebrae (41 most frequent) . . . . ***P. magdalenae***
(rivers of northern Colombia)

Body with series of dark, wavy, horizontal stripes; scales in lateral line 44 to 51 (45 to 48 most frequent); 14 to 22 median predorsal scales (16 to 18 most frequent); 41 to 44 vertebrae (42 or 43 most frequent) (basins of Rio São Francisco, Río de La Plata, and Rio Paraiba do Sul) 11

11. Median predorsal scales 14 to 20 (16 most frequent); vertebrae 42 to 44 (43 most frequent) . . . . ***P. lineatus***
(Río de La Plata and Rio Paraíba do Sul basins)

Median predorsal scales 14 to 22 (17 or 18 most frequent); vertebrae 42 to 44 (42 most frequent) (basin of Rio São Francisco) 12

12. Horizontal rows of scales between dorsal-fin origin and lateral line 10 or 11 .... ***P. argenteus***
(originally endemic to the basin of Rio São Francisco, but now introduced into various rivers of northeastern Brazil)

Horizontal rows of scales between dorsal-fin origin and lateral line 8 or 9 .... ***P. costatus***
(basin of Rio São Francisco; reported to have been introduced in the Rio Jequitinhonha system)

Chave de Identificação das Espécies de *Prochilodus*

1. Nadadeira caudal com 2 a 8 fileiras verticais irregulares e sinuosas de pequenas manchas negras formadas por agrupamentos de cromatóforos, pigmentação ocasionalmente ausente em *P. brevis;* ver comentários na descrição da espécie (Río Orinoco, Río Amazonas, Rios costeiros das Guianas, Rios costeiros do nordeste do Brasil entre São Luís e Salvador, incluindo afluentes setentrionais do baixo Rio São Francisco) 2

Nadadeira caudal hialina (rios do norte da Colômbia, bacia do Lago Maracaibo, Rio São Francisco, rios costeiros do Brasil entre o Rio Pardo, Bahia, e o Rio Paraíba do Sul, Rio de Janeiro, Rio Apiacá da bacia do Rio Juruena, bacia do Rio da Prata) 6

2. Linha lateral com 52–64 escamas (52 extremamente raro, 1 caso apenas) .... ***P. mariae***
(bacia do Río Orinoco)

Linha lateral com 41–52 escamas (52 raro, 2 casos apenas) (Río Caroni, Río Amazonas, rios costeiros das Guianas, rios costeiros do nordeste do Brasil entre São Luís e Salvador, incluindo afluentes setentrionais do baixo Rio São Francisco) 3

3. Escamas no corpo com padrão cruciforme de subdivisões radiais, geralmente uma estendendo-se dorsalmente e outra ventralmente e algumas vezes também uma outra estendendo-se anterior e posteriormente, porem sem padrão complexo de subdivisões secundárias [Figura 24] (rios costeiros do nordeste do Brasil, incluindo afluentes setentrionais do baixo Rio São Francisco) 4

Escamas no corpo com padrão complexo de subdivisões secundárias em adição ao padrão regular de linhas radiais; padrão complexo presente não em todas escamas e mais comum em indivíduos de porte maior [Figura 25] (bacias dos Rios Amazonas, Tocantins, Branco e Marauiá, Río Caroni e rios costeiros das Guianas) 5

4. Linha lateral com 41–48 escamas (43 mais freqüente, 46–48 incomuns); 6–8 fileiras horizontais de escamas da origem da nadadeira pélvica à linha lateral (7 mais freqüente, 8 incomum) [Figura 37] .... ***P. brevis***
(rios costeiros de porte pequeno a médio nordeste do Brasil, incluindo afluentes setentrionais do baixo Rio São Francisco)

Linha lateral com 46–51 escamas (47 mais freqüente); 8–11 fileiras horizontais de escamas da origem da nadadeira pélvica à linha lateral (9 mais freqüente, 8 incomum) [Figura 37] .... ***P. lacustris***
(bacias dos Rios Parnaíba e Mearim no NE do Brasil)

5. Fileiras horizontais de escamas em torno do pedúnculo caudal 17–21 (19 mais freqüente, 17 e 18 incomuns); 7–9 fileiras horizontais de escamas da origem da nadadeira pélvica à linha lateral (8 mais freqüente) [Figura 55] ..... ***P. nigricans***
(bacia Amazônica e bacia do Rio Tocantins)

Fileiras horizontais de escamas em torno do pedúnculo caudal 14–18 (16 mais freqüente, 17, 18 incomum); 6–7 fileiras horizontais de escamas da origem da nadadeira pélvica à linha lateral (6 mais freqüente) [Figura 55] .... ***P. rubrotaeniatus***
(bacias dos Rios Branco e Marauiá, Río Caroni, e rios costeiros das Guianas)

6. Escamas na linha lateral 34–39 .... ***P. vimboides***
(rios costeiros do Brasil entre os Rios Jucurucu e Paraíba; cabeceiras dos afluentes do alto Rio Paraná e Rio São Francisco)
Escamas na linha lateral 40–51 (rios do norte da Colômbia, bacia do lago Maracaibo, Rio São Francisco, Rios Pardo e Jequitinhonha, Bahia, Río Apiaca da bacia do Rio Juruena, bacia do Rio da Prata) 7
7. Dentes na fileira interna da metade da maxila inferior 6–7; menor altura do pedúnculo caudal 8.8%–9.4% do comprimento padrão .... ***P. britskii***
(Rio Apiacá, afluente do Rio Juruena)
Dentes na fileira interna da metade da maxila inferior 8–18; menor altura do pedúnculo caudal maior que 9.5% do comprimento padrão (rios do norte da Colômbia, bacia do lago Maracaibo, Rio São Francisco, Rios Pardo e Jequitinhonha, Bahia, bacia do Rio da Prata) 8
8. 14–16 fileiras horizontais de escamas em torno do pedúnculo caudal; escamas na linha lateral 40–43; 13–18 dentes na fileira interna da metade da maxila inferior ... . ***P. hartii***
(bacias dos Rios Pardo e Jequitinhonha, NE Brasil)
16–22 fileiras horizontais de escamas em torno do pedúnculo caudal; escamas na linha lateral 41–51; 8–18 dentes na fileira interna da metade da maxila inferior (rios do norte da Colômbia, bacia do lago Maracaibo, Rio São Francisco, bacia do Rio da Prata) 9
9. Escamas na linha lateral 41–45 (43 mais frequente); 11–18 escamas pré-dorsais medianas (13 mais frequente); 38–40 vértebras (39 mais frequente) ..... ***P. reticulatus***
(bacia do Lago Maracaibo)
Escamas na linha lateral 43–51 (valores mais frequentes 44–48); 12–22 escamas pré-dorsais medianas (valores mais frequentes 15–18); 39–44 vértebras (valores mais frequentes 41–43) (rios do norte da Colômbia, Rio São Francisco, bacia do Rio da Prata) 10
10. Corpo desprovido de linhas sinuosas escuras horizontais; escamas na linha lateral 43–46 (44 mais frequente); 12–17 escamas pré-dorsais medianas (15 mais frequente); 39–41 vértebras (41 mais frequente) .... ***P. magdalenae***
(rios do norte de Colômbia)
Corpo com linhas sinuosas escuras horizontais; escamas na linha lateral 44-51 (valores mais frequentes 45–48); 14–22 escamas pré-dorsais medianas (valores mais frequentes 16–18); 41–44 vértebras (valores mais frequentes 42–43) (bacias dos Rio São Francisco, Rio de Prata e Rio Paraíba do Sul) 11
11. Escamas pré-dorsais medianas 14–20 (16 mais frequente); vértebras 42–44 (43 mais frequente) .... ***P. lineatus***
(bacias do Rio da Prata e Rio Paraíba do Sul)
Escamas pré-dorsais medianas 14–22 (valores mais frequentes 17 e 18); vértebras 42–44 (42 mais frequente) (bacia do Rio São Francisco) 12
12. Fileiras transversais de escamas da origem da nadadeira dorsal à linha lateral 10–11 . ... ***P. argenteus***
(bacia do Rio São Franciscoe introduzido emdiversos rios no nordeste do Brasil)
Fileiras transversais de escamas da origem da nadadeira dorsal à linha lateral 8–9 .. .. ***P. costatus***
(bacia do Rio São Francisco, e aparentemente introduzido no Rio Jequitinhonha, Brasil)

Prochilodus argenteus Agassiz, 1829

FIGURE 30, 32; TABLE 5

Prochilodus argenteus Agassiz in Spix and Agassiz, 1829:63, pl. 38 [type locality: S. Francisci (=Brazil, Rio São Francisco), restricted herein to Brazil, Minas Gerais, Januária, Rio São Francisco; neotype locality: Brazil, Bahia, Rio Desidério, São Desidério, near Barreiras].—Valenciennes in Cuvier and Valenciennes, 1850:71 [Rio San-Francisco (=Rio São Francisco)].—Lütken, 1875b:189 [in part, specimens from Rio das Velhas; not synonymy of *P. costatus*].—Cope, 1878:686 [cited as similar to *P. cephalotes*].—Eigenmann and Ogle, 1907:5 [cited similarity to *P. beani*].—Eigenmann, 1910:424 [in listing of South American fishes; in part, not synonymy of *Prochilodus costatus*]; 1912:271 [purported similarity to *P. maripicru* noted]; 1917:23 [equivalence of *Curimata* Marcgrave to *P. argenteus*].—Steindachner, 1915:21 [in part, specimens from Rio São Francisco at Barra and Sambaiba, not cited specimens from Parnahyba (=Rio Parnaíba)].—Azevedo and Vieira, 1938:8, unnumbered figure facing page 9 [ecology, feeding, growth, reproduction, anatomy].—Angelescu and Gneri, 1949:175 [feeding, based upon Azevedo and Vieira, 1938].—Travassos, 1952:225 [as type species of *Prochilodus*].—Braga, 1961:20 [Brazil, Pernambuco, Rio Moxoto].—Géry, 1963:392 [request to International Commission on Zoological Nomenclature]; 1977:222 [in part, not synonymy of *P. costatus* and *P. lacustris* into *P. argenteus;* not occurrence of *P. argenteus* in Rio Parnahyba (=Parnaíba), Brazil].—Lowe-McConnell, 1964:121 [possible total spawner, based upon literature information]; 1975:219 [fecundity]; 1987, table 11.3 [number of ova].—International Commission on Zoological Nomenclature, 1966:41 [opinion involving available names for synonyms of species].—Roberts, 1973b:214 [sound production during spawning migrations].—Nomura, 1984:54 [Brazil, common name].—Pauls and Bertollo, 1984:787 [karyotype].—Petrere, 1985:7 [importance in Amazonian fishery]; 1989:8 [economic importance].—Bertollo et al., 1986:156, table 1 [karyotype].—Nakatani et al., 2001:182, figs. 51, 52 [descriptions of eggs and larval stages].—Alves and Pompeu, 2001:82, 184 [Brazil, basin of Rio das Velhas].—[Not Günther, 1864:294; Lütken, 1875b:189; Eigenmann and Eigenmann, 1891:48; Perugia, 1891:640; Pearson, 1937b:109; Bertoni, 1939:59; Ringuelet, 1975:72; Lopez et al., 1987:18.]

Pacu argenteus.—Agassiz in Spix and Agassiz, 1829:63 [as synonym of *Prochilodus argenteus*].—Müller and Troschel, 1844:84 [Brazil]; 1845:8 [Brazil].

Prochilodus steindachneri [not of Fowler, 1906].—Fowler, 1941:171 [in part, Brazil, Rio São Francisco; not Ceará, Rio Salgado, Icó]; 1950:224 [in part, Brazil, Rio São Francisco; not Ceará, Rio Salgado, Icó].—Nomura, 1984:54 [Brazil, common name].

Salmo marggravii.—Fowler, 1950:215 [in part, as synonym of type species of *Prochilodus* Agassiz in Spix and Agassiz, 1829 (=*Prochilodus argenteus*); name suppressed by International Commission on Zoological Nomenclature (1966: opinion 772)].

Prochilodus marggravii.—Fowler, 1950:220 [in part, name suppressed by International Commission on Zoological Nomenclature (1966: opinion 772)]; 1975:359 [literature compilation, not synonymy of *P. costatus*].—Mago-Leccia, 1972:47 [use of caudal-fin pigmentation to discriminate groups of species].—Britski et al., 1984:59 [Brazil, Rio São Francisco]; 1986:59 [Brazil, Rio São Francisco].—Menin and Mimura, 1991:229 [details of epibranchial anatomy].—Santos and Barbieri, 1991:5 [age and growth].—Menin and Mimura, 1992:507 [buccopharyngeal anatomy]; 1993:253 [stomach anatomy].—Sato and Godinho, 1999:404, 411, table 17.3 [Brazil, Rio São Francisco; biology and ecology].—[Not Godoy, 1987:180 (incorrect synonymy into *Prochilodus platensis*).]

Prochilodus margravei.—Ringuelet et al., 1967:204 [Río de La Plata basin; biological data; unjustified emendation of name suppressed by International Commission on Zoological Nomenclature (1966: opinion 772)].—Nomura, 1984:54 [Brazil, common name].

Prochilodus brevis [not of Steindachner, 1874].—Nomura, 1984:54 [Brazil, common name].

Prochilodus margravii.—Pauls and Bertollo, 1984:787 [unjustified emendation of name suppressed by International Commission on Zoological Nomenclature (1966: opinion 772); karyotype].—Bertollo et al., 1986:156, table 1 [karyotype].

Prochilodus marggravi.—Géry et al., 1987:438 [incorrect spelling of name suppressed by International Commission on Zoological Nomenclature (1966: opinion 772)].

DIAGNOSIS.—*Prochilodus argenteus* differs from *P. mariae, P. brevis, P. rubrotaeniatus, P. lacustris,* and *P. nigricans* in having a hyaline caudal fin rather than having the dark, irregular, wavy bar-like patterns present on the caudal-fin lobes in those five species. Within the group of *Prochilodus* species with hyaline caudal fins, *P. argenteus* differs from *P. vimboides* in the number of scales along the lateral line (45 to 51 versus 34 to 39, respectively); from *Prochilodus britskii* in the number of horizontal rows of scales between the dorsal-fin origin and the lateral line (10 or 11 versus 6 or 7, respectively) and in the number of horizontal rows of scales around the caudal peduncle (17 to 22 versus 13 or 14, respectively); from *P. costatus* in the number of horizontal rows of scales between the dorsal-fin origin and the lateral line (10 or 11, 11 rows most frequent, versus 8 or 9, 9 rows most frequent, respectively); from *P. hartii* in the number of horizontal rows of scales between the dorsal-fin origin and the lateral line (10 or 11 versus 6 to 8, respectively) and in the number of scales along the lateral line (45 to 51 versus 40 to 43, respectively); from *P. lineatus* in the number of horizontal rows of scales between the dorsal-fin origin and the lateral line (10 or 11, 11 rows most frequent, versus 7 to 10, 9 rows most frequent and 10 relatively rare, respectively; Figure 33), the number of median predorsal scales (17 to 22, 18 and 19 most frequent and 20 and 21 almost as frequent, versus 14 to 20, 16 scales most frequent and 19 to 21 scales relatively infrequent, respectively; Figure 34), the number of scales along the lateral line (45 to 51, 48 most frequent, versus 44 to 50, 47 scales most frequent, respectively), and the number of vertebrae (42 or 43, 42 most frequent, versus 42 to 44, 43 most frequent, respectively); from *P. magdalenae* in the presence of wavy, dark, longitudinal stripes along the body (stripes absent in *P. magdalenae*), in the number of scales between the dorsal-fin origin and the lateral line (10 or 11 versus 8 or 9, respectively), and the number of vertebrae (42 to 44 versus 39 to 41, respectively); and from *P. reticulatus* in the presence of wavy, dark, longitudinal stripes along the body (stripes absent in *P. reticulatus*), in the number of horizontal rows of scales between the dorsal-fin origin and the lateral line (10 or 11 versus 7 to 9, respectively), the number of vertebrae (42 to 44 versus 38 to 40, respectively), the number of scales along the lateral line (45 to 51, 48 most frequent, versus 41 to 45, 43 most frequent, respectively), and the number of median predorsal scales (17 to 22, 18 most frequent, versus 11 to 18, 13 most frequent, respectively).

DESCRIPTION.—Morphometric and meristic data for *Prochilodus argenteus* presented in Table 5. Body relatively high and transversely compressed. Greatest body depth at dorsal-fin origin. Dorsal profile of head gently concave. Predorsal

TABLE 5.—Morphometrics and meristics of *Prochilodus argenteus:* (A) neotype of *Prochilodus argenteus* (MZUSP 28778), and (B) all specimens of *Prochilodus argenteus* from which counts and measurements were taken. Standard length is presented in mm; values 2 to 16 are percentages of SL, 17 to 21 are percentages of HL.

Character	A	B
	Morphometrics	
1. Standard length	237.0	57.6–436.5
2. Greatest body depth	37.0	35.4–44.0
3. Predorsal length	47.7	44.9–51.9
4. Dorsal-fin base length	18.8	17.6–19.9
5. Dorsal fin to adipose fin distance	25.4	21.7–26.8
6. Dorsal fin to caudal fin distance	47.3	37.0–50.0
7. Prepelvic length	50.7	46.9–57.1
8. Preanal distance	77.6	73.6–82.3
9. Snout to anal-fin insertion	80.0	77.6–83.9
10. Anal-fin base length	11.7	9.6–14.8
11. Caudal-peduncle length	13.1	11.2–14.8
12. Dorsal-fin length	31.9	27.3–40.1
13. Pectoral-fin length	19.2	16.3–22.6
14. Pelvic-fin length	18.4	13.9–24.0
15. Least caudal-peduncle height	13.2	11.5–14.6
16. Head length	28.5	22.8–35.9
17. Snout length	44.4	35.6–46.5
18. Bony orbital diameter	23.2	17.7–30.4
19. Postorbital length	39.2	35.4–43.8
20. Interorbital width	53.6	47.8–58.6
21. Mouth width	44.5	42.9–49.2
	Meristics	
Lateral-line scales	44	45–51
Scale rows between dorsal-fin origin and lateral line	10	10–11
Scale rows between anal-fin origin and lateral line	6	6–8
Scale rows between pelvic-fin insertion and lateral line	8	7–9
Rows of scales around caudal peduncle	18	17–22
Median predorsal scales	20	17–22
Median scales between dorsal and adipose fins	14	13–17
Vertebrae	43	42–44
Inner row teeth, upper jaw	22	15–25
Inner row teeth, lower jaw	11	8–14

profile of body convex. Body profile posteroventrally inclined at dorsal-fin base. Profile ranging from gently convex to straight in region from posterior of dorsal-fin base to adipose-fin origin and concave along caudal peduncle. Predorsal portion of body with slight median ridge. Postdorsal portion of body transversely obtusely rounded. Ventral profile of body moderately convex from tip of lower jaw to posterior of anal-fin base. Ventral profile of caudal peduncle concave. Prepelvic region transversely flattened proximate to pelvic-fin insertion. Distinct keel present between pelvic-fin insertion and anus.

Head profile pointed. Snout length greater than horizontal width of orbit. Nares of each side of head close to each other; anterior nares circular, posterior nares crescent shaped. Adipose eyelid present but poorly developed; eyelid most highly developed anteriorly, but with major portion of eye uncovered. Lips fleshy, moderately developed, and forming oral disk when protracted.

Functional teeth in two rows in each jaw. All teeth movably implanted in flesh that overlies jaws. All teeth of similar size and spoon shaped except when worn down. Inner tooth series in each jaw with 15 to 25 teeth on left side of upper jaw and 8 to 14 teeth on left side of lower jaw. Outer row of teeth in each jaw with approximately 83 teeth on each side of upper jaw and approximately 72 teeth on each side of lower jaw in neotype. Upper and lower lips bordered by numerous globular, fleshy papillae.

Scales spinoid. Scales in middorsal series between posterior of dorsal-fin base and adipose-fin origin similar in form to those of adjoining regions of body. Lateral line with 45 to 51 (35.7% of specimens with 48) pored scales; 10 or 11 (64.3% of specimens with 11) horizontal rows of scales between dorsal-fin origin and lateral line; 7 to 9 (60.7% of specimens with 8) horizontal rows of scales between pelvic-fin insertion and lateral line; 6 to 8 (75.0% of specimens with 7) horizontal rows of scales between anal-fin origin and lateral line; 17 to 22 (50.0% of specimens with 18 or 19) median predorsal scales; 13 to 17 (39.3% of specimens with 14) scales in middorsal series between posterior of dorsal-fin base and adipose-fin origin; 17 to 22 (85.7% of specimens with 18) horizontal rows of scales around caudal peduncle.

Dorsal fin preceded by small, anteroventrally bifurcate, procumbent spine somewhat triangular in lateral view. Dorsal-fin rays (including procumbent spine) iii,10 [iii,10]; anal-fin rays ii,8 or iii,8 (iii,8 most frequent) [ii,8]; pectoral-fin rays i,13 to 16 (i,14 most frequent) [i,14]; pelvic-fin rays i,8 [i,8]; principal caudal-fin rays 10/9 [10/9].

Vertebrae 42 to 44 (57.1% of specimens with 42).

Dorsal fin truncate and slightly pointed distally; three anterior branched rays longest and subequal. Dorsal-fin origin located closer to tip of snout than to caudal-fin base. Greatest length of adipose fin approximately two-thirds of horizontal width of orbit. Adipose-fin origin located along vertical that passes through middle of anal-fin base. Pectoral fin distally pointed. Tip of adpressed pectoral fin reaching posteriorly almost to pelvic-fin insertion. Pelvic fin falcate. Pelvic-fin origin located along vertical that passes approximately through anterior one-fourth of dorsal-fin base. Tip of adpressed pelvic fin reaching posteriorly approximately two-thirds of distance between pelvic-fin insertion and anus. Axillary scale present, its length approximately two-thirds of greatest length of pelvic fin. Posterior unbranched and anterior branched rays of anal fin longest and subequal. Caudal fin moderately bifurcate.

COLORATION IN ALCOHOL.—Ground coloration silvery yellow or brownish yellow, with dorsal portions of body and head darker. Lateral surface of body with 5 to 17 (most frequently 12) vertical, dark, diffuse, patches between rear of head and caudal fin. Patches with approximate overall form of narrow isosceles triangles with apexes positioned in center of ventrolateral portion of body and bases along dorsomedial region of

FIGURE 32.—*Prochilodus argenteus*, neotype, MZUSP 28778, 237.0 mm SL; Brazil, Bahia, Rio Desidério, São Desidério, near to Barreiras.

body. Patches well developed in juveniles and small adults; indistinct or absent in large individuals. Lateral surface of body with approximately 5 to 15 (most frequently 12) dark, wavy, horizontal stripes along dorsal and ventral margins of exposed portions of scales. Approximately 5 to 7 (most frequently 5) wavy stripes above, and 0 to 8 (most frequently 6) stripes below, lateral line. Patch of black or brown chromatophores forming irregular, dark patch on upper one-half of opercle.

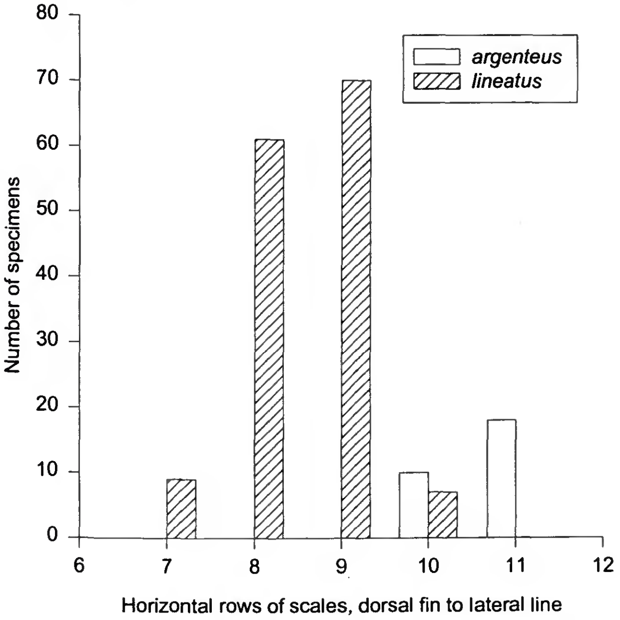


FIGURE 33.—Histogram of number of horizontal rows of scales between dorsal-fin insertion and lateral line plotted against number of specimens with particular counts in *Prochilodus argenteus* and *Prochilodus lineatus*.

Dorsal fin with 4 to 10 irregular dark stripes beginning at anterior margin of fin and extending across fin approximately parallel to fin base. Adipose fin with small, diffuse, dark spots and with fin margin finely bordered with black. Pectoral, pelvic, anal, and caudal fins dusky. Iris golden yellow, with diffuse dusky areas on dorsal and ventral portions.

DISTRIBUTION.—*Prochilodus argenteus* was originally endemic to, and widely distributed through, the Rio São Francisco basin of eastern, Brazil (Figure 30, dots). The species was subsequently introduced into various river basins of northeastern Brazil by the Departamento Nacional de Obras Contra as Secas (DNOCS). One lot examined but not indicated on the distribution map (ANSP 75489) from Ceará, Icó, Rio Salgado apparently represents a sample of such an introduced population.

COMMON NAME.—Curimatã, curimatã-pacu (Brazil).

COMPARISONS.—As indicated in the "Diagnosis," above, *Prochilodus argenteus* of the Rio São Francisco basin of eastern Brazil unequivocally differs in one or more features from all congeners with the exception of *P. lineatus* of the Río de La Plata and Rio Paraíba do Sul basins. The two nominal forms, although demonstrating some overlap in the number of median predorsal scales and in the number of horizontal rows of scales between the lateral line and the dorsal-fin origin, nonetheless demonstrate pronounced differences in the modal counts for these values (see Figure 34 for median predorsal scales). In light of those differences and the allopatry of the nominal forms, we recognize them as distinct species in this study.

REMARKS.—*Prochilodus argenteus*, the type species of *Prochilodus*, was described by Agassiz (in Spix and Agassiz, 1829:63–64, pl. 38). The description was based, at least in part, upon a specimen of approximately 395.0 mm, which had been collected by Spix and Martius in the Rio São Francisco, Brazil, probably in the city of Januária, Minas Gerais (see Portugese

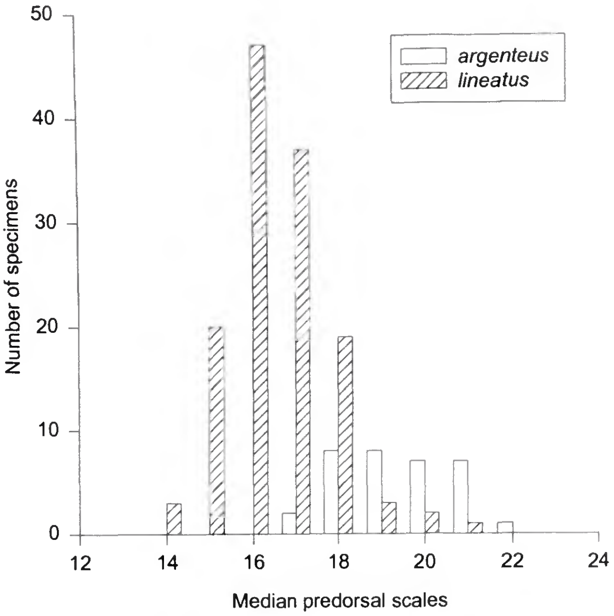


FIGURE 34.—Histogram of number of median predorsal scales plotted against number of specimens with particular counts in *Prochilodus argenteus* and *Prochilodus lineatus.*

translation (1976:85–87) of Spix and Martius, 1823–1831; see also Papavero, 1971:65–69, map 7 for itinerary of that collecting expedition). As noted by Kottelat (1988:69), "the specimens collected by Spix (except those subsequently given to Agassiz) were housed in the Zoologische Staatssammlung München until their destruction by a British bombing raid on the night of 24–25 April 1944." Kottelat (1988:84) did not list the holotype of *P. argenteus* as being in any museum known to house portions of the Spix collections, and no types for the species were cited by Eschmeyer et al. (in Eschmeyer, 1998:134). In all likelihood, the holotype of *P. argenteus* is no longer extant.

Agassiz (in Spix and Agassiz, 1829:63) reported the presence of 52 lateral-line scales in *Prochilodus argenteus,* a value close to the range of 45 to 51 pored lateral-line scales present in the examined specimens identified herein as *P. argenteus.* Three other *Prochilodus* species are known to occur in the Rio São Francisco system: *P. brevis, P. costatus,* and *P. vimboides. Prochilodus brevis* typically has distinct pigmentation on the caudal fin, contrary to the hyaline caudal fin of *P. argenteus. Prochilodus vimboides,* in turn, has 34 to 39 scales along the lateral line, a much different range for this feature than in *P. argenteus.* The last species, *P. brevis* is most similar overall to *P. argenteus,* but it has 44 to 47 scales along the lateral line, a different range than the value for that feature cited by Agassiz for *P. argenteus.* Nonetheless, the two nominal forms are quite similar and, as is amply demonstrated by the synonymy for *P. argenteus,* this species has been repeatedly confounded with various other similar *Prochilodus* species, some of which have comparable lateral line counts. In order stabilize the nomenclature of the species, we herein designate a neotype for *Prochilodus argenteus.* The neotype (MZUSP 28778, 237 mm SL, Rio Desidério, São Desidério, near Barreiras) originated in the central portion of Rio São Francisco basin where the holotype of the species was apparently collected (see comments above and Figure 30).

The name *Prochilodus marggravii* has been applied by various authors to *Prochilodus argenteus* (see listing within synonymy, above). That species name is, however, unavailable, having been placed by the International Commission on Zoological Nomenclature (1966:45, opinion 772) on the Official Index of Rejected and Invalid Names and Works in Zoology.

Various authors (see listing in species synonymy, above) erroneously considered *P. costatus* and *P. lacustris* to be junior synonyms of *P. argenteus.* Both *P. costatus* and *P. lacustris* differ from *P. argenteus* in various features (see "Diagnosis," above) and are considered distinct herein. *Prochilodus cephalotes,* originally described from the Peruvian Amazon, was cited by Steindachner (1915:21) as a junior synonym of *P. argenteus.* The results of this study indicate that *P. cephalotes* is instead a junior synonym of *P. nigricans,* a species endemic to the Amazon basin. *Prochilodus steindachneri,* a junior synonym of *P. vimboides,* was erroneously applied by Fowler (1941:171) to specimens from the Rio São Francisco basin that we find are an admixture of *P. argenteus* and *P. brevis.*

MATERIAL EXAMINED.—70 specimens (24, 57.6–436.5 mm SL).

NEOTYPE.—BRAZIL. *Bahia:* Rio Desidério, Município de São Desidério, near Barreiras, collected by M.A. Castarolli and J. Camargo, 2–6 May 1985, MZUSP 28778, 1 (1, 237.0, neotype of *Prochilodus argenteus;* designated herein).

BRAZIL. *Bahia:* Barra, Rio São Francisco, NMW 56605, 2 (2, 232.8–298.6); NMW 56606, 4 (2, 72.2–78.6); NMW 56641, 1 (1, 316.8); NMW 56643, 3 (2, 189.2–287.3); NMW 56725, 4 (2, 57.6–74.1); NMW 56854:1–2, 2 (1, 85.6–87.7). Confluence of Rio Grande with Rio São Francisco, Barra, FMNH 92992, 1 (181.0). Penedo, mouth of Rio São Francisco, FMNH 78098, 1 (110.0); FMNH 92293, 1 (129.3); FMNH 92994, 1 (74.5); FMNH 93007, 1 (100.6). Rio Desidério, Município de São Desidério, near Barreiras, MZUSP 55638, 1 (231.5; collected with neotype and formerly MZUSP 28778, neotype lot, in part). Rio São Francisco, MZUSP 2040, 1 (1, 180.0). *Ceará:* Icó, Rio Salgado (this lot probably represents an introduction into that region of *P. argenteus* by the Departamento Nacional de Obras Contra as Secas, DNOCS, and is not shown on the distribution map, Figure 30), ANSP 75489, 1 (1, 87.1) [1R]. Propriá, Rio São Francisco, MZUSP 21519, 1 (1, 172.2). *Minas Gerais:* Riacho and Lago de Mocambinho, right margin of Rio São Francisco, Município de Manga (14°46′S, 43°56′W), MZUSP 41278, 2 (cleared and counterstained for bone and cartilage); MZUSP 42073, 4 (84.3–147.7). Rio São Francisco and tributaries, vicinity of Usina Hidrelétrica Formoso project, MZUSP 39740, 6 (223.6–319.7). Três Marias, Rio São Francisco,

MZUSP 21453, 2 (2, 278.0–322.0); MZUSP 21717, 4 (4, 203.0–246.0); MZUSP 42673, 1 (1, 122.2). Rio São Francisco, between Guaicuí and Januária, MCZ 20162, 2 (172.9–173.0); MCZ 20290, 1 (93.4). Rio das Velhas, upriver of Belo Horizonte, BMNH 1925.6.9:2, 1 (436.5). *Pernambuco:* Jatobá, Rio São Francisco, ANSP 75488, 4 (1, 78.6–90.6) [1R]. Temporary lagoon along Rio São Francisco, 9.6 km from Juazeiro, FMNH 76363, 2 (197.2–225.4). Lago Coripo or Carijós, near Santa Maria da Boa Vista, Rio São Francisco, UMMZ 147404, 5 (1, 125.9–165.1) [2R]; USNM 161329, 9 (105.6–304.0). Samambaia (approximately 25 km N of Ibimirim), NMW 56644, 2 (1, 69.0–70.5).

Prochilodus brevis Steindachner, 1874

FIGURES 30, 35; TABLE 6

Prochilodus brevis Steindachner, 1874:536 (page 38 of separate), pl. 6 [type locality: Flüsse in der Umgebung von Bahia (=river in the region of Bahia), more specifically Brazil, Bahia, Salvador (see "Remarks," below), restricted herein to Brazil, Bahia, basin of Rio Paraguaçu].—Eigenmann and Eigenmann, 1891:48 [in listing of South American fishes].—Eigenmann and Ogle, 1907:5 [cited similarity to *P. beani*].—Eigenmann, 1907b:768 [lateral-line scale count]; 1910:424 [in listing of South American fishes].—Mago-Leccia, 1972:47 [use of caudal-fin pigmentation to discriminate groups of species].—Fowler, 1975:358 [literature compilation].—Géry, 1977:219 [Bahia].—Nakatani et al., 2001:188, figs. 53, 54 [descriptions of eggs, larval, and juvenile stages].

Prochilodus cearensis Steindachner, 1911:329 [type locality: Flusschen bei Ipú im Staate Ceará (=Brazil, Ceará, river in Ipú)].—Fowler, 1941:171 [as possible synonym of, or closely related to, *P. hartii*]; 1975:358 [literature compilation].—Mago-Leccia, 1972:47 [use of caudal-fin pigmentation to discriminate group of species].—Géry, 1972b:33 [compared with *Curimatus* (= *Prochilodus*) *tigris*].—Nomura, 1984:54 [Brazil, common name].—Petrere, 1989:8 [economic importance]. New Synonomy.

Prochilodus nigricans [not of Agassiz, 1829].—Fowler, 1915:262; 1950:221 [in part, eastern Brazilian citations and reported distribution of species].—Nomura, 1984:54 [Brazil, common name].

Prochilodus argenteus [not of Agassiz, 1829].—von Ihering and Azevedo, 1934:143 [in part, cited occurrence in portions of northeastern Brazil, life history, fecundity, artificial breeding].

Prochilodus corimbata [not of Kner, 1859].—Fowler, 1941:169 [Brazil, Lago Paparey (= Papari), Rio Grande do Norte; Fortaleza, Ceará; Campina Grande, Parahyba (=Paraíba)].—Géry, 1972b:33 [erroneously suggested as senior synonym of *Curimatus* (=*Prochilodus*) *tigris*]; 1977:218 [in part, not synonymy of *P. cearensis*].

Prochilodus oligolepis [not of Günther, 1864].—Fowler, 1941:169 [under synonymy of *Prochilodus corimbata* (Kner, 1859)].

Salmo corimbata [not of Kner, 1859].—Fowler, 1941:169 [under synonymy of *Prochilodus corimbata* (Kner, 1859)].

Prochilodus curimbata [not of Kner, 1859].—Nomura, 1984:54 [unjustified emendation of species name; Brazil, common name].

Prochilodus steindachneri [not of Fowler, 1906].—Nomura, 1984:54 [Brazil, common name].

DIAGNOSIS.—*Prochilodus brevis* differs from *P. argenteus, P. britskii, P. costatus, P. hartii, P. lineatus, P. magdalenae, P. reticulatus,* and *P. vimboides* in its possession of a series of dark, irregular, bar-like patterns on the caudal-fin lobes that contrast with the hyaline caudal fins in those eight species. Within the group of *Prochilodus* species with such a pattern of dark caudal-fin pigmentation, *P. brevis* differs from *P. mariae* in the number of scales along the lateral line (41 to 48 versus 52 to 64, respectively) and in the number of scale rows from the dorsal-fin origin to the lateral line (7 to 9 versus 10 or 11, respectively); from *P. lacustris* in the number of horizontal rows of scales between the pelvic-fin insertion and the lateral line (6 to 8, 7 most frequent and 8 infrequent, versus 8 to 11, 9 most frequent and 8 infrequent, respectively; Figure 36), the number of scales along the lateral line (41 to 48, 43 most frequent and 46 to 48 infrequent, versus 46 to 51, 47 most frequent and 46 in only 17% of specimens examined for this feature, respectively; Figure 37), and the number of vertebrae (40 to 42, with 40 and 41 most common and 42 in only 6.7% of specimens examined for this feature, versus 41 to 43, with 42

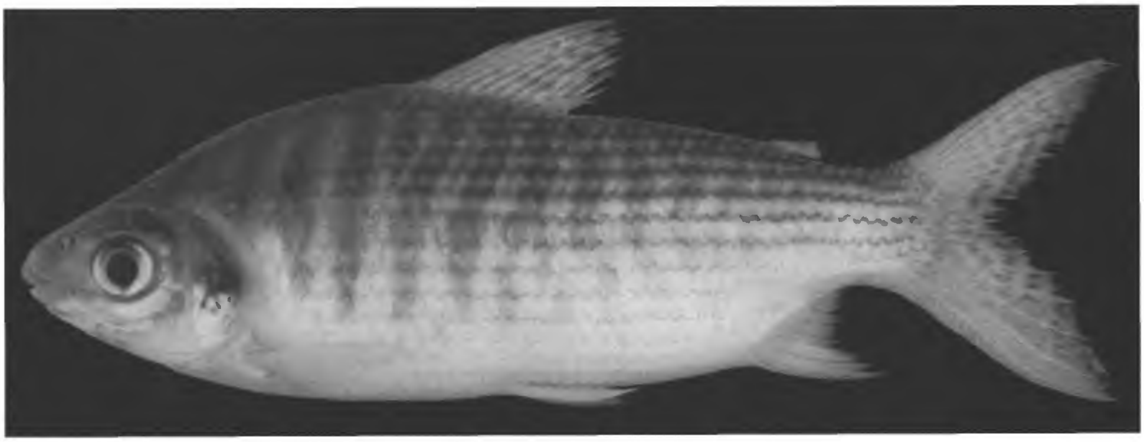


FIGURE 35.—*Prochilodus brevis*, MZUSP 42678, 111.6 mm SL; Brazil, Bahia, Lagoa Charca Natividade, near Iaçu.

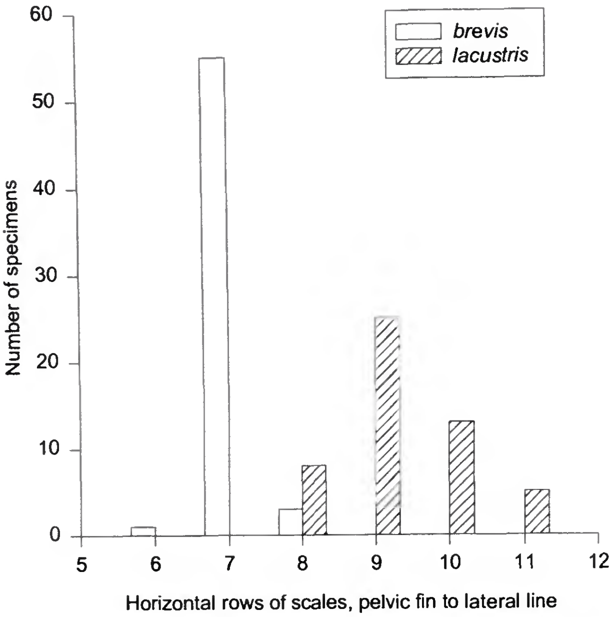


FIGURE 36.—Histogram of number of horizontal rows of scales between pelvic-fin insertion and lateral line plotted against number of specimens with particular counts in *Prochilodus brevis* and *Prochilodus lacustris*.

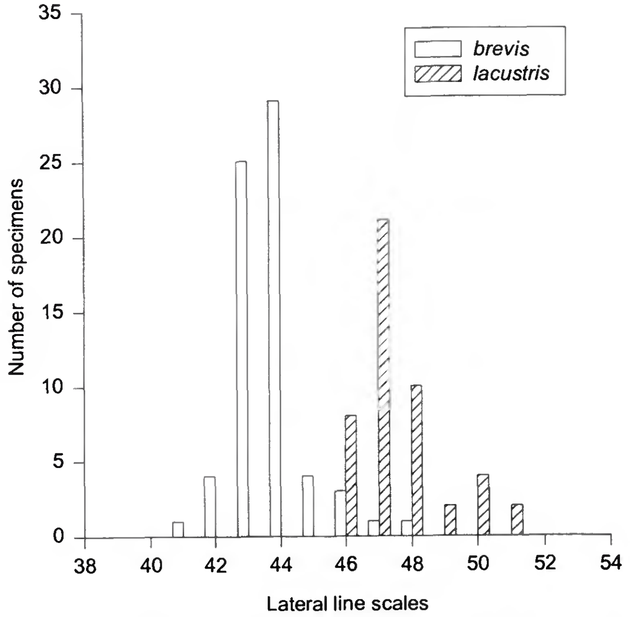


FIGURE 37.—Histogram of number of lateral-line scales plotted against number of specimens with particular counts in *Prochilodus brevis* and *Prochilodus lacustris*.

most common and 41 in only 1 of 13 specimens examined for this feature, respectively; Figure 38); from *P. nigricans* in the form of the scales (with only radial subdivisions versus having complex pattern of variable subdivisions; see Figure 25 for latter condition), the number of scales along the lateral line (41 to 48, 43 and 44 in 76.3% of specimens, versus 44 to 51, 48 most frequent with 44 in only 1 of 236 specimens examined for this feature and 45 not found in examined specimens, respectively), and the number of horizontal rows of scales between the pelvic-fin insertion and the lateral line (6 to 8, 7 in 93.2% of specimens, versus 7 to 9, with 8 in 50.7% of specimens and 7 in 17.4% of specimens, respectively); and from *P. rubrotaeniatus* in scale form (with only radial subdivisions versus having complex pattern of variable subdivisions; see Figure 25 for latter condition) and in the number of scales along the lateral line (41 to 48, with 43 and 44 in 76.3% of specimens and 45 to 48 infrequent, versus 44 to 48, 46 most frequent and 44 rare, respectively).

DESCRIPTION.—Morphometric and meristic data for *Prochilodus brevis* presented in Table 6. Body moderately high, transversely compressed. Greatest body depth at dorsal-fin origin. Dorsal profile of head gently concave to straight. Predorsal profile of body gently convex. Body profile posteroventrally inclined at dorsal-fin base; slightly convex from posterior of dorsal-fin base to adipose-fin origin, and concave along caudal peduncle. Predorsal portion of body with slight median ridge. Postdorsal portion of body obtusely rounded transversely. Ventral profile of body gently convex from tip of lower jaw to posterior of anal-fin base. Ventral profile of caudal peduncle concave. Prepelvic region transversely flattened proximate to pelvic-fin insertion. Moderately developed me-

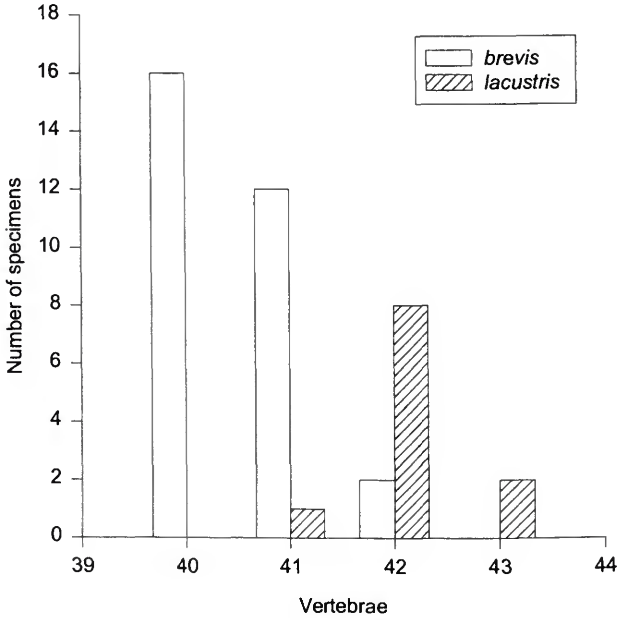


FIGURE 38.—Histogram of number of vertebrae plotted against number of specimens with particular counts in *Prochilodus brevis* and *Prochilodus lacustris*.

TABLE 6.—Morphometrics and meristics of *Prochilodus brevis:* (A) lectotype of *Prochilodus brevis*, NMW 56638; (B) paralectotypes of *Prochilodus brevis*, NMW 56636:1–4; (C) lectotype of *Prochilodus cearensis*, NMW 56640:2; (D) paralectotypes of *Prochilodus cearensis*, NMW 56640:1, NMW 56639:1–2; and (E) all specimens of *Prochilodus brevis* from which counts and measurements were taken. Standard length is presented in mm; values 2 to 16 are percentages of SL, 17 to 21 are percentages of HL.

Characters	A	B	C	D	E
			Morphometrics		
1. Standard length	119.1	83.6–98.6	147.5	134.6–138.3	56.0–270.0
2. Greatest body depth	42.1	41.4–45.1	34.1	34.1–35.3	31.9–45.4
3. Predorsal length	49.0	48.1–52.4	48.2	46.7–48.3	44.3–53.0
4. Dorsal-fin base length	18.1	17.4–18.5	16.3	16.3–16.8	15.0–19.1
5. Dorsal fin to adipose fin distance	26.5	24.8–27.6	24.7	23.6–24.7	20.7–31.6
6. Dorsal fin to caudal fin distance	42.7	42.3–43.6	42.4	39.8–42.8	39.1–48.4
7. Prepelvic length	51.1	51.3–55.4	52.4	52.2–52.4	49.9–57.4
8. Preanal distance	74.8	74.2–77.6	78.6	77.3–78.6	73.7–81.7
9. Snout to anal-fin insertion	77.7	78.0–82.1	81.9	80.5–81.9	77.1–85.6
10. Anal-fin base length	12.0	10.6–14.0	10.8	10.7–11.4	9.0–14.7
11. Caudal-peduncle length	10.3	13.3–14.4	12.4	12.4–14.6	10.3–16.7
12. Dorsal-fin length	32.0	32.7–40.9	30.3	27.4–30.3	24.1–40.9
13. Pectoral-fin length	20.1	17.6–23.9	21.0	19.5–21.0	14.6–33.4
14. Pelvic-fin length	20.8	18.8–23.4	18.1	17.5–18.1	14.2–24.0
15. Least caudal-peduncle height	13.1	13.5–13.9	12.3	12.3–12.7	10.6–14.3
16. Head length	28.8	29.4–31.8	28.9	28.9–29.1	24.1–32.3
17. Snout length	39.1	35.9–37.6	38.0	38.0–41.6	24.7–44.6
18. Bony orbital diameter	27.4	26.6–32.0	23.0	23.0–23.6	18.7–40.5
19. Postorbital length	37.6	35.9–39.3	41.5	39.8–43.1	35.8–47.2
20. Interorbital width	55.4	53.4–56.5	52.3	51.0–55.1	51.0–59.0
21. Mouth width	46.9	43.1–44.7	43.3	43.3–45.1	38.1–49.9
			Meristics		
Lateral-line scales	43	42–43	44	44–45	41–48
Scale rows between dorsal-fin origin and lateral line	9	8–9	9	8–9	7–9
Scale rows between anal-fin origin and lateral line	6	6–7	7	6–7	5–8
Scale rows between pelvic-fin insertion and lateral line	7	7	7	7	6–8
Rows of scales around caudal peduncle	18	16–18	18	18–18	15–18
Median predorsal scales	15	15–17	16	16–17	12–17
Median scales between dorsal and adipose fins	16	13–14	15	14–15	12–16
Vertebrae	40	40–41	41	40–41	40–42
Inner row teeth, upper jaw	19	20–23	15	14–15	13–23
Inner row teeth, lower jaw	11	10–11	8	8	8–11

dian keel present between pelvic-fin insertion and anus.

Head profile pointed. Mouth terminal. Snout length greater than horizontal width of orbit. Nares of each side of head close to each other; anterior nares circular, posterior nares crescent shaped. Adipose eyelid present but very poorly developed; most developed along anterior border of eye, but with greater part of eye uncovered. Lips fleshy, moderately developed relative to some other prochilodontids, and forming oral disk when protracted.

Functional teeth in two rows in each jaw. All teeth movably implanted in flesh that overlies jaws, of similar size, and with visible portion spoon shaped except when worn down. Inner tooth series in each jaw with 13 to 23 teeth on left side of upper jaw and 8 to 11 teeth on left side of lower jaw. Outer row of teeth in each jaw with approximately 74 teeth on each side of upper jaw and approximately 57 teeth on each side of lower jaw in lectotype. Upper and lower lips bordered by numerous globular, fleshy, papillae.

Scales spinoid. Scales in middorsal series between posterior of dorsal-fin base and adipose-fin origin similar in form to those of adjoining regions of body. Lateral line with 41 to 48 (42.4% of specimens with 43) pored scales; 7 to 9 (69.5% of specimens with 8) horizontal rows of scales between dorsal-fin origin and lateral line; 6 to 8 (93.2% of specimens with 7) horizontal rows of scales between pelvic-fin insertion and lateral line; 5 to 8 (64.4% of specimens with 6) horizontal rows of scales between anal-fin origin and lateral line; 12 to 17 (46.5% of specimens with 15) median predorsal scales; 12 to 16 (45.4% of specimens with 14) scales in middorsal series between posterior of dorsal-fin base and adipose-fin origin; 15 to 18 (37.3% of specimens with 16) horizontal rows of scales around caudal peduncle.

Dorsal fin preceded by small, but well developed, anteroventrally bifurcate, procumbent spine somewhat triangular in lateral view. Dorsal-fin rays (including procumbent spine) iii,9 to 11 (iii,10 most frequent) [iii,10]; anal-fin rays iii,7 to 9, or ii,7 to 9 (iii,8 most frequent) [iii,8]; pectoral-fin rays i,13 to 15 (i,14 most frequent) [i,14]; pelvic-fin rays i,8 [i,8]; principal caudal-fin rays 10/9 [10/9].

Vertebrae 40 to 42 (53.3% of specimens with 40).

Dorsal fin truncate distally; posterior unbranched and anterior branched rays longest and subequal. Dorsal-fin origin located closer to tip of snout than to caudal-fin base. Greatest length of adipose fin approximately equal to horizontal width of orbit. Adipose-fin origin located along vertical that passes through approximately anterior one-third of length of anal-fin base. Pectoral fin distally pointed. Tip of adpressed pectoral fin reaching posteriorly approximately three-fourths of distance between pectoral- and pelvic-fin insertions. Pelvic fin falcate. Pelvic-fin origin located along vertical that passes through anterior one-third of dorsal-fin base. Tip of adpressed pelvic-fin extending posteriorly approximately three-fourths of distance between pelvic-fin insertion and anus. Axillary scale present, its length approximately one-fourth of greatest length of pelvic fin. Posterior unbranched and anterior branched anal-fin rays longest and subequal. Caudal fin bifurcate.

COLORATION IN ALCOHOL.—Ground coloration silvery yellow or brownish yellow, with dorsal portion of body and head darker. Lateral surface of body typically with 8 to 13 dark, diffuse, irregular, vertical patches between head and caudal fin. Patches with approximate overall form of narrow isosceles triangles with apexes located along center of ventrolateral portion of body and bases on dorsomedial region of body. Patches very obvious in juveniles and smaller specimens, but indistinct or absent in larger individuals. Lateral surface of body with approximately 8 to 13 dark, wavy, horizontal stripes along dorsal and ventral margins of exposed portions of scales. Approximately 4 to 7 (most frequently 5) wavy stripes above lateral line, and 4 to 6 (most frequently 5) below. Stripes somewhat irregular on caudal peduncle. Field of black or brown chromatophores forming dark, irregular pigmentation patch on upper one-half of opercle.

Dorsal fin with 3 to 7 (most frequently 5) dark, irregular, stripes beginning at anterior margin of fin and extending across fin approximately parallel to base of fin. Adipose fin with margin finely marked with black. Pectoral, pelvic, and anal fins hyaline. Caudal fin in most specimens with 3 to 5 (most frequently 3) irregular vertical bars and wavy patterns of small, black spots formed of groups of chromatophores (Note: approximately 6% of specimens that originated in the Rio Paraguaçu, Bahia, Brazil, lack this dark caudal-fin pigmentation, and it is faint in approximately 17% of that sample; see comments under 'Remarks," below). Iris yellowish silver, with diffuse dusky areas on dorsal and ventral portions.

COLORATION IN LIFE.—(Based upon color transparency of a recently collected specimen from the Rio Paraguaçu basin taken by the first author and a transparency of a specimen from the Rio Jaquaribe, near Lima Campos, Ceará, Brazil, provided by Flavio A. Bockmann, LIRP). Dark pigmentation as described above. Ground coloration silvery, with dorsal portion of body and particularly head much darker. Overall coloration of fins with reddish pigmentation, otherwise hyaline. Posterior margins of anal and caudal fins slightly reddish. Pectoral and particularly pelvic fins with coloration more orange than red. Larger specimen from the Rio Jaquaribe with posterior margins of scales outlined with dark pigmentation and with interradial membranes of anal fin distinctly dark. Lateral surface of head in that specimen somewhat golden.

DISTRIBUTION.—*Prochilodus brevis* is known from the small to medium-sized coastal rivers of northeastern Brazil and from small northern tributaries of the lower portion of the Rio São Francisco (Figure 30, triangles).

COMMON NAME.—Curimatã-comum (Brazil).

COMPARISONS.—*Prochilodus brevis* is readily distinguishable from all congeners except *P. lacustris, P. nigricans,* and *P. rubrotaeniatus* by the combination of differences in caudal-fin pigmentation and the non-overlapping ranges of meristic features cited in the "Diagnosis," above. *Prochilodus brevis* of eastern and northeastern Brazil differs from *P. nigricans* of the Rio Amazonas and Rio Tocantins basins and from *P. rubrotaeniatus* of the Guianas and northern portions of the Rio Negro basin in the form of the scales on the body (with only radial subdivisions versus typically having complex pattern of variable subdivisions, respectively; see discussion of feature under "Scales" in "Character Description and Analysis") and in various modal meristic values, most notably in the number of scales along the lateral line. *Prochilodus brevis* differs from *P. lacustris,* also of northeastern Brazil, in its slightly overlapping, but modally distinct, ranges for the number of horizontal scale rows between the pelvic-fin insertion and the lateral line (6 to 8 scales in that series in *P. brevis,* with 8 scales in that series in only 3 of 59 specimens from which that count was taken, versus 8 to 11 scales in that series in *P. lacustris,* with 8 scales in only 8 of the 51 specimens from which that count was taken; Figure 36) and in the number of scales along the lateral line (Figure 37) and in the number of vertebrae (Figure 38). In light of the allopatric distribution of *P. brevis* and *P. lacustris* and the cited differences, we herein recognize them as distinct species.

REMARKS.—In his original description of *Prochilodus brevis,* Steindachner (1874:536–538, pl. 6) failed to identify the type specimens for the species and inexactly reported the type locality as "river in the region of Bahia" (our translation). The introductory comments to that publication noted that Steindachner visited the Museum of Comparative Zoology (MCZ) for a period during 1869–1870 in order to examine the fishes collected by the Thayer expedition in Brazil. Steindachner returned to the Naturhistorisches Museum, Vienna (NMW) with portions of the Thayer collection and reported on specimens from that material in a series of papers during the following decades.

Searches through the holdings of MCZ and NMW revealed the presence of three lots of *Prochilodus brevis* of similar size and condition that apparently jointly constitute an originally single sample from the Thayer Expedition. Information with the MCZ sample (MCZ 20160, 8 specimens) indicates that it was collected by Hartt and Copeland, members of the Thayer Expedition, at "Bahia." The specimens at NMW (NMW 56636, 4 specimens; NMW 56638, 1 specimen) also originated at that location, but no information on the collector is associated with those lots. According to Higuchi (1996), the Thayer Expedition collecting locality cited as "Bahia" by authors, including Steindachner, is more exactly the city of Salvador and its environs in the state of Bahia, Brazil. The major river in the vicinity of the city of Salvador is the Rio Paraguaçu, and the sampling of its ichthyofauna in the course of this study has demonstrated that *P. brevis* is present in that river basin (see comments below).

The two lots of *Prochilodus brevis* at NMW (NMW 56636, NMW 56638) are, however, labeled as "Prochilodus bahiensis," a species name that apparently has never been published (Eschmeyer et al., in Eschmeyer, 1998). In other instances, Steindachner changed the species names for forms he described in the interval between his identification of the material as representing a form apparently unknown to science and the formal description of the species (see comments in Vari, 1991:50). Such action apparently transpired with the NMW specimens identified as "Prochilodus bahiensis."

The specimens in the two NMW lots match Steindachner's original description of *P. brevis* and are consequently considered to represent the syntypes of that species. The single specimen in NMW 56638, 119.1 mm SL, that is in the best overall condition, is herein designated as the lectotype of *P. brevis,* and the other four syntypes (NMW 56636:1–4, 83.6–98.6 mm SL) consequently become paralectotypes of that species. There is no indication that Steindachner utilized the specimens in MCZ 20610 in his original description of *P. brevis,* and those specimens are consequently not considered to represent part of the type series of that species.

A striking aspect of the illustration of *Prochilodus brevis* included in the original description of the species (Steindachner, 1874, pl. 6) is the absence of the dark caudal-fin markings that were considered typical of that species. Furthermore, Steindachner failed to mention dark caudal-fin pigmentation for that species in the text, despite his remark (1874:538) that dark spots are present on the dorsal fin of *P. brevis.* Dark caudal-fin pigmentation is, furthermore, absent on the lectotype and paralectotypes of *P. brevis* and in the nontype lot (MCZ 20160) that originally included the type series. The absence of dark caudal-fin pigmentation in these samples was at first perplexing in light of the presence of the feature in all of the other, then-available, specimens of what was apparently *P. brevis.* Notwithstanding the lack of any nonpigmentary differences between the typeseries of *P. brevis* and the other available samples of the species, the variation in the caudal-fin pigmentation raised questions about the conspecificity of the type series with what were apparently other samples of *P. brevis* that originated from the type region.

Subsequent field work provided further insight into the significance of these apparent differences in caudal-fin pigmentation. Collecting activities in the Rio Paraguaçu basin of Bahia yielded a total of 69 specimens of *Prochilodus brevis.* Approximately 6% of the specimens in that sample have a hyaline caudal fin without any indication of dark marks, a situation comparable to that in the typeseries of the species. Approximately 17% of the specimens in this sample have limited numbers of variably poorly developed dark marks on the caudal fin, whereas the remaining approximately 77% of the specimens have variably distinct, but obvious dark marks on the caudal-fin lobes. Because of the continuity in the degrees of development of the caudal-fin pigmentation within the Rio Paraguaçu population samples, including the type series of *P. brevis,* we consider the samples to be conspecific, albeit with variable degrees of expression of this dark pigmentation (see Table 6). *Prochilodus brevis* represents the only instance we encountered within the Prochilodontidae of such intraspecific variation in caudal-fin pigmentation among comparably sized specimens. Whether the consistent absence of caudal-fin pigmentation in the original series of *P. brevis* was a consequence of some conscious decision during the selection of specimens for preservation or only the chance collection of specimens that lacked such pigmentation, a condition that, however, now occurs in only a small percentage of the specimens of *P. brevis* in that river basin, cannot be determined.

Steindachner's (1911:329–330) description of *Prochilodus cearensis* was based upon four specimens collected by Snethlage at "Flusschen bei Ipú im Staate Ceará" (=river in Ipú, Ceará, Brazil; our translation). No differences were identified between the type series of *P. cearensis* and examined samples of *P. brevis* (see Table 6). *Prochilodus cearensis* is consequently considered to be a junior synonym of *P. brevis.* Four specimens identified as the syntypes of *Prochilodus cearensis* are known to be extant in the NMW holdings. Of these, we designate the largest individual (NMW 56640:2, 147.5 mm SL), which is in the best overall condition, as the lectotype of the species, and the three other syntypes (NMW 56639:1–2, 134.6–137.4 mm SL; NMW 56640:1, 138.3 mm SL) consequently become paralectotypes of the species.

Fowler (1915, 1941) reported on various collections of prochilodontids from northeastern Brazil under diverse specific names (see species synonymy, above). The examination of the material that served as the basis for various of these citations indicates that all of them, except for those samples from the rios Parnaíba and Grajaú, refer to *P. brevis.*

MATERIAL EXAMINED.—160 specimens (61, 56.0–270.0 mm SL).

BRAZIL. *Alagoas:* Lagoa do Mundaú, Maceió, MZUSP 4211, 3 (22.6–28.2); MZUSP 37550, 5 (3, 125.4–153.3);

MZUSP 42667, 3 (3, 152.5–164.2); MZUSP 42674, 5 (4, 93.9–121.8); MZUSP 42675, 2 (2, 157.8–178.0). Camurupim, Maceió, MZUSP 42112, 4 (22.8–24.7). Rio Mundaú, São José da Lage (9°01′S, 36°03′W), MZUSP 42100, 1 (139.9). Mouth of Rio Paraíba do Meio, Pilar, MZUSP 42114, 2 (70.7–105.2). *Bahia:* Salvador and vicinity (probably Rio Paraguaçu basin; see under "Remarks," above), MCZ 20160, 8 (8, 82.7–99.5); NMW 56636:1–4, 4 (4, 83.6– 98.6, paralectotypes of *Prochilodus brevis*) [4]; NMW 56638, 1 (1, 119.1, lectotype of *Prochilodus brevis*) [1R]. Lagoa Charca Natividade, near Iaçu, MZUSP 42678, 14 (5, 89.8–125.7) [13R]; USNM 319768, 14 (2, 56.0–88.7). Município de Itaetê, Olho d'Aqua do Almerindo, tributary of Rio Una, Rio Paraguaçu basin, approximately 18 km SE of Andarai, LIRP 769, 1. Riacho Madalena, near Iaçu (12°45′S, 40°12′W), MZUSP 42679, 21 (5, 57.2–83.60); MZUSP 42717, 2 (cleared and counterstained for bone and cartilage); USNM 319770, 20 (2, 100.4–110.9). "Ferry boat" [crossing], Rio Jacuípe, MZUSP 38862–63, 2 (2, 106.1–155.3). *Ceará:* córrego in Ipu, NMW 56639:1–2, 2 (2, 134.6–137.4, paralectotypes of *Prochilodus cearensis*) [2R]; NMW 56640:2, 1 (1, 147.5, lectotype of *Prochilodus cearensis*) [1R]; NMW 56640:1, 1 (1, 138.3, paralectotype of *Prochilodus cearensis*) [1R]. Fortaleza, ANSP 69476–9, 4 (1, 64.8–91.6) [1R]; ANSP 82290, 1 (270.0); ANSP 90636, 1 (1, 214.7) [1R]. Açude São Bento, Fortaleza, UMMZ 203534, 1 (1, 160.4) [1R]. Rio Jaguaribe, in Morro Alto, ANSP 39921-22, 2 (1, 101.7–109.9) [1R]. Rio Jaguaribe, in Orós, ANSP 12489, 3 (112.6–177.5). Icó, USNM 163258, 3 (3, 217.7–241.9) [1R]. No explicit locality, MZUSP 21433, 5 (5, 98.4–108.0). Riacho do Umbuzeiro, near Aiuaba (6°38′S, 40°07′W), MZUSP 37584, 14 (80.1–106.1). *Paraíba:* Campina Grande, ANSP 90635, 1 (1, 231.7). Bodocongó, Campina Grande, ANSP 84627, 2 (88.5–90.6). *Pernambuco:* Riacho do Gentio, tributary of Riacho Alegre, Riacho das Garças drainage, Rio São Francisco basin (8°14′30.8″S, 40°19′20.2″W), LIRP 3781, 1 (77.9). Município de Trindade, Riacho de Conceição, tributary of Riacho São Pedro, Rio São Francisco basin (7°51′27″S, 40°22′47″W), LIRP 4010, 1 (84.8). *Rio Grande do Norte:* Lago Papari, ANSP 95872, 3 (1, 122.4–142.5); ANSP 96051, 2 (1, 174.2–214.6) [1R].

Prochilodus britskii **Castro, 1993**

FIGURES 30, 39; TABLE 7

Prochilodus bristkii Castro, 1993:57, fig. 1 [type locality: Brazil, Mato Grosso, Rio Apiacá (tributary of Rio Arinos, Rio Tapajós basin) N of city of Juará, upriver from a fall (~10°36′S, 58°04′W)].—Oyakawa, 1996:492 [holotype and paratype depository].

DIAGNOSIS.—*Prochilodus bristkii* is distinguished from all of its congeners by its relatively shallow caudal-peduncle height (8.8% to 9.4% of SL versus 9.7% or greater in all other *Prochilodus* species). It is further distinguished from *P. brevis, P. lacustris, P. mariae, P. nigricans,* and *P. rubrotaeniatus* by the lack of dark, irregular, wavy, bar-like patterns on the caudal-fin lobes that are present in those five species. *Prochilodus britskii* may be separated from other *Prochilodus* species that lack dark caudal-fin pigmentation by the presence of 6 or 7 teeth in the inner tooth row of each side of the lower jaw versus 8 to 18 teeth in that series among most congeners with hyaline fins, with the exception of *P. vimboides,* which has 6 to 13 teeth in that series. *Prochilodus bristkii* differs from *P. vimboides* in various features, most distinctly in the number of scales along the lateral line (41 to 44 versus 34 to 39, respectively). *Prochilodus britskii* demonstrates two osteological features (the secondary tube that extends from the ventral border of the primary laterosensory canal in the first infraorbital and the single tubular ossification located ventral of the quadrate and anterior of the preopercle) that may represent autapomorphies for the species. We qualify that statement because of the distinctly larger size of the single cleared and stained specimen of *P. brit-*

TABLE 7.—Morphometrics and meristics of *Prochilodus britskii:* (A) holotype of *Prochilodus britskii,* MZUSP 41519; (B) paratypes of *Prochilodus britskii;* and (C) all specimens of *Prochilodus britskii* from which counts and measurements were taken. Standard length expressed in mm; measurements 1 to 15 are percentages of SL; 16 to 20 are percentages of HL.

Characters	A	B	C
		Morphometrics	
1. Standard length	221.5	195.5–238.5	195.5–238.5
2. Greatest body depth	29.1	28.9–30.3	28.9–30.3
3. Predorsal length	47.2	45.6–47.4	45.6–47.4
4. Dorsal-fin base length	14.6	14.3–16.2	14.3–16.2
5. Dorsal fin to adipose fin distance	29.4	27.5–30.2	27.5–30.2
6. Dorsal fin to caudal fin distance	42.5	41.7–43.7	41.7–43.7
7. Prepelvic length	54.4	53.9–55.1	53.9–55.1
8. Preanal distance	75.5	76.5–79.0	75.5–79.0
9. Snout to anal-fin insertion	77.9	78.2–81.3	77.9–81.3
10. Anal-fin base length	10.5	8.4–10.4	8.4–10.5
11. Caudal-peduncle length	13.9	12.5–13.8	12.5–13.9
12. Dorsal-fin length	24.2	23.3–25.3	23.3–25.3
13. Pectoral-fin length	20.5	18.3–21.3	18.3–21.3
14. Pelvic-fin length	16.7	15.1–16.5	15.1–16.7
15. Least caudal-peduncle height	9.3	8.8–9.4	8.8–9.4
16. Head length	26.1	25.7–26.2	25.7–26.2
17. Snout length	38.4	36.4–42.6	36.4–42.6
18. Bony orbital diameter	18.9	17.4–20.6	17.4–20.6
19. Postorbital length	44.1	41.2–45.7	41.2–45.7
20. Least interorbital width	47.9	46.2–49.2	46.2–49.2
21. Gape width	39.8	38.7–39.9	38.7–39.9
		Meristics	
Lateral-line scales	44	41–43	41–44
Scale rows between dorsal-fin origin and lateral line	7	6–7	6–7
Scale rows between anal-fin origin and lateral line	6	5–6	5–6
Scale rows between pelvic-fin insertion and lateral line	7	6–7	6–7
Scale rows around caudal peduncle	14	13–14	13–14
Median predorsal scales	14	13–14	13–14
Median scales between dorsal and adipose fins	14	13–15	13–15
Vertebrae	41	40–41	40–41
Inner row teeth, upper jaw	13	10–13	10–13
Inner row teeth, lower jaw	7	6–7	6–7

FIGURE 39.—*Prochilodus britskii*, holotype, MZUSP 41519, 221.5 mm SL; Brazil, Mato Grosso, Rio Apiacá, north of Juara.

skii relative to the cleared and stained specimens of other members of the genus.

DESCRIPTION.—Morphometric and meristic data for *Prochilodus bristkii* presented in Table 7. Body relatively elongate, subcylindrical, greatest body depth at dorsal-fin origin. Caudal peduncle notably shallow. Dorsal profile of head slightly concave to straight. Dorsal profile of body slightly convex predorsally. Body profile slightly posteroventrally slanted along dorsal-fin base; slightly convex from posterior of dorsal-fin base to adipose-fin origin, and slightly concave along caudal peduncle. Predorsal portion of body with very slightly developed median ridge. Postdorsal portion of body transversely rounded. Ventral profile of body gently convex from tip of lower jaw to termination of anal-fin base, slightly concave along caudal peduncle. Prepelvic region moderately flattened transversely proximate to pelvic-fin insertion. Slight mid-ventral keel present between pelvic-fin insertion and anus.

Head pointed in profile. Mouth terminal. Snout length exceeding horizontal eye diameter. Nostrils of each side of head close together, anterior nares circular, posterior nares crescent shaped. Adipose eyelid present but scarcely developed; most pronounced anteriorly, but with greater portion of eye uncovered. Fleshy lips forming oral disk when protruded.

Functional teeth in two rows in each jaw. All teeth movably implanted in flesh that overlies jaws. All teeth of similar size, with exposed portion spoon shaped in frontal view, except when worn down. Inner tooth series in each jaw with 10 to 13 [13] teeth on left side of upper jaw and 6 or 7 [7] teeth on left side of lower jaw. Outer row of teeth in each jaw with approximately 73 teeth on each side of upper jaw and approximately 60 teeth on each side of lower jaw in holotype. Upper and lower lips bordered by numerous small, globular, fleshy papillae.

Scales spinoid. Scales along dorsal midline between posterior termination of dorsal fin and adipose-fin origin comparable in form to those of adjoining regions of body, without spatulate membranous process along posterior margin of each scale in that series. Lateral line with 41 to 44 (43% of specimens with 41, 29% with 42) [44] pored scales; 6 or 7 (71% of specimens with 7) [7] horizontal rows of scales from dorsal-fin origin to lateral line; 6 or 7 (57% of specimens with 7) [7] horizontal rows of scales from pelvic-fin insertion to lateral line; 5 or 6 (71% of specimens with 5) [6] horizontal rows of scales from anal-fin origin to lateral line; 13 or 14 (71% of specimens 14) [14] median predorsal scales; 13 to 15 [14] median scales between posterior of dorsal-fin base and adipose-fin origin; 13 or 14 [14] horizontal scale rows around caudal peduncle.

Dorsal fin preceded by small, anteroventrally bifurcate, procumbent spine. Dorsal-fin rays (including procumbent spine) iii,9 or 10 (iii,9 rare) [iii,10]; anal-fin rays iii,8 [iii,8]; pectoral-fin rays i,13 or 14 (i,14 most frequent) [i,13]; pelvic-fin rays i,8 [i,8]; principal caudal-fin rays 10/9 [10/9].

Vertebrae 40 or 41 (40 most frequent).

Dorsal fin truncate distally; posterior unbranched and anterior branched rays longest and subequal. Dorsal-fin origin located nearer to tip of snout than to caudal-fin base. Longest length of adipose fin approximately equal to, or slightly longer than, horizontal width of orbit. Origin of adipose fin located along vertical that passes just anterior of posterior termination of anal-fin base. Pectoral fin distally pointed. Tip of adpressed pectoral fin reaching approximately two-thirds of distance between pectoral-fin and pelvic-fin insertions. Pelvic fin falcate. Pelvic-fin origin located along vertical that passes through midpoint of dorsal-fin base. Tip of adpressed pelvic fin reaching approximately four-fifths of distance to anus. Axillary scale present, pointed, its length about one-third of pelvic-fin length. Posterior unbranched and anterior branched rays of anal fin longest and subequal. Caudal fin forked.

COLOR IN ALCOHOL.—Ground coloration silvery yellow to silvery brown on dorsal half of body and head. Approximately seven very diffuse vertical bands on sides of body between head and caudal fin; bands formed by chromatophore fields without distinct limits. Lateral surface of body lacks wavy, dark, horizontal stripes present in many congeneric species. Field of black or brown chromatophores forming irregularly shaped spot on dorsal one-half of opercle.

Dorsal fin with irregularly distributed, diffuse, and barely visible small dark spots. Adipose fin with central region dusky and dorsal margin black. Pectoral, pelvic, and anal fins mostly hyaline, with distal portions somewhat dusky. Iris silvery yellow, with dorsal and ventral portions dusky.

COLORATION IN LIFE.—Shortly after its collection, the type series of *Prochilodus britskii* demonstrated strong reddish yellow coloration on the pelvic, anal, and caudal fins (Heraldo A. Britski, MZUSP, pers. comm., 1987).

DISTRIBUTION.—*Prochilodus britskii* is only known from the type locality, the Rio Apiacá, a tributary of Rio Arinos, which is, in turn, a tributary of Rio Juruena of the upper Rio Tapajós system, Mato Grosso, Brazil (Figure 30, square). The species may have a more extensive distribution in that river basin, possibly occurring in the upper Rio Arinos basin at Fazenda Fervedouro (14°13'S, 56°01'W), a locality where it, or a similar species, has been observed living at the base of rapids on that river (H.R. Mendes, Universidade de São Paulo; Ribeirão Preto, pers. comm., 2001). Even if that reported range extension is confirmed, the known distribution of *P. britskii* still would be the most restrictive of any *Prochilodus* species.

COMPARISONS.—As noted in the "Diagnosis," the relative caudal-peduncle depth serves to unequivocally distinguish *P. britskii* from its congeners. *Prochilodus britskii* also differs from all congeners in the overall form of its head and body.

MATERIAL EXAMINED.—7 specimens (7, 195.5–238.5 mm SL).

BRAZIL. *Mato Grosso:* Rio Apiacá, tributary of Rio Arinos, Rio Tapajós basin, N of Juara, upriver from a water fall (~10°36'S, 58°04'W), MZUSP 38856–38861, 6 (195.5–238.5, paratypes of *Prochilodus britskii;* MZUSP 38856 (cleared and counterstained for cartilage and bone) [R]; MZUSP 41519, 1 (221.5 mm SL, holotype of *Prochilodus britskii*) [R].

***Prochilodus costatus* Valenciennes, 1850**

FIGURES 40, 43; TABLE 8

Prochilodus costatus Valenciennes in Cuvier and Valenciennes, 1850:79 [type locality: Brazil, Rio San-Francisco du Brésil (=Rio São Francisco, Brazil), restricted herein to Brazil, Minas Gerais, Rio São Francisco].—Casatti and Castro, 1998:232, table 1, fig. 4d [Rio São Francisco headwaters, species survey and ecology].—Godinho et al., 1999:423 [introduction of species into Rio Jequitinhonha basin, eastern Brazil; common name].—Nakatani et al., 2001:193, figs. 55, 56 [descriptions of eggs, larval, and juvenile stages].—Alves and Pompeu, 2001:82, 184 [Brazil, basin of Rio das Velhas].—[Not Eigenmann, 1910:424; synonymy of *P. costatus* into *P. argenteus* or cited occurrence of *P. costatus* in Rio Paraguay basin.]

Prochilodus argenteus [not of Agassiz, 1829].—Günther, 1864:294 [in part, erroneous inclusion of *P. costatus* as a synonym of *P. argenteus*].—Lütken, 1875b:189 [in part, erroneous synonymy of *P. costatus* into *P. argenteus*].—Eigenmann and Eigenmann, 1891:48 [in listing of South American fishes].—Géry, 1977:219 [in part, occurrence in Rio São Francisco basin, but not synonymy of *P. costatus* into *P. argenteus*].—Nomura, 1984:54 [Brazil, common name].—[Not Steindachner, 1915:21; possible synonymy of *P. costatus* into *P. argenteus*.]

Prochilodus affinis Lütken, 1875a:128 (page 2 of separate) [type locality: Rio das Velhas et rivulis affluentibus (= Brazil, Minas Gerais, Rio das Velhas and tributaries, Rio São Francisco basin), restricted by Fowler (1950:215) to Brazil, Minas Gerais, Rio das Velhas]; 1875b:189 [based upon Lütken, 1875a].—Eigenmann and Eigenmann, 1891:48 [in listing of South American fishes].—Eigenmann, 1910:424 [in listing of South American fishes].—Fowler, 1950:215 [in part, not cited occurrence in Rio Paraguai]; 1975:357 [literature compilation].—Braga, 1961:21, table 6 [Brazil, Pernambuco; apparently introduced, but identification questionable because of typical use of *P. argenteus* in introductions of prochilodontids by Departamento Nacional de Obras Contra as Secas].—Mago-Leccia, 1972:47 [use of caudal-fin pigmentation to identify species groups].—Nielsen, 1974:48 [syntype depository].—Géry, 1977:222 [in part, only Rio São Francisco citation].—Britski et al., 1984:59 [Brazil, Rio São Francisco].—Nomura, 1984:54 [Brazil, common name].—Pauls and Bertollo, 1984:787 [karyotype].—Bertollo et al., 1986:156, table 1 [karyotype].—Britski et al., 1986:59 [Brazil, Rio São Francisco].—Santos and Barbieri, 1991:6 [age and growth].—Menin and Mimura, 1991:229 [details of epibranchial anatomy]; 1992:507 [buccopharyngeal anatomy]; 1993:253. [stomach anatomy].—Sato and Godinho, 1999:411, table 17.3 [Brazil, Rio São Francisco basin].—Alvez and Pompeu, 2001:82 [translation of Lütken, 1875b].—Britski, 2001:20 [as synonym of *Prochilodus costatus* based upon Castro, 1990]. New synonomy.

Pacu argenteus [not of Agassiz, 1829].—Fowler, 1950:221 [in part, in synonymy of *Prochilodus marggravii,* name suppressed by the International Commission on Zoological Nomenclature (1966: opinion 772)].

Prochilodus marggravii.—Fowler, 1975:359 [*Prochilodus costatus* incorrectly cited as synonym of *P. marggravii* (=*P. argenteus*)].

Prochilodus lineatus.—Géry, 1977:219 [in part, cited occurrence in Rio São Francisco but not reported distribution outside that river basin].

Prochilodus brevis [not of Steindachner, 1874].—Nomura, 1984:54 [Brazil, common name].

Prochilodus steindachneri [not of Fowler, 1906].—Nomura, 1984:54 [Brazil, common name].

DIAGNOSIS.—*Prochilodus costatus* differs from *P. brevis*, *P. lacustris*, *P. mariae, P. nigricans*, and *P. rubrotaeniatus* in its lack of dark, irregular, wavy, bar-like patterns on the caudal-fin lobes that occur in those five species. Within the group of *Prochilodus* species without black marks on the caudal fin, *P. costatus* differs from *P. vimboides* in the number of scales along the lateral line (44 to 47 versus 34 to 39, respectively) and in the number of horizontal rows of scales between the dorsal-fin origin and the lateral line (8 or 9 versus 5 to 7, respectively); from *P. britskii* in the number of horizontal rows of scales around the caudal peduncle (16 to 18 versus 13 or 14, respectively) and in the number of teeth in the inner row of each side of the lower jaw (10 to 14 versus 6 or 7, respectively); from *P. hartii* in the number of scales along the lateral line (44 to 47, 45 most frequent, versus 40 to 43, 41 most frequent, respectively) and in the number of vertebrae (41 to 43, 42 most frequent, versus 37 to 40, 40 most frequent, respectively); from *P. argenteus* in the number of horizontal rows of scales between the dorsal-fin origin and the lateral line (8 or 9, 9 most frequent, versus 10 or 11, 11 most frequent, respectively); from *P. reticulatus* in the possession of a series of wavy, dark, horizontal stripes on the lateral surface of the body (stripes absent in *P. reticulatus*), the number of vertebrae (41 to 43, versus 38 to 40, respectively), the number of predorsal median scales (14 to 18, 17 most frequent and 14 rare, versus 11 to 18, 16 and 18 rare and 17 not represented in counted specimens), and the number of lateral-line scales (44 to 47, 45 most frequent and 44 rare, versus 41 to 45, 42 and 43 most frequent and 45 rare);

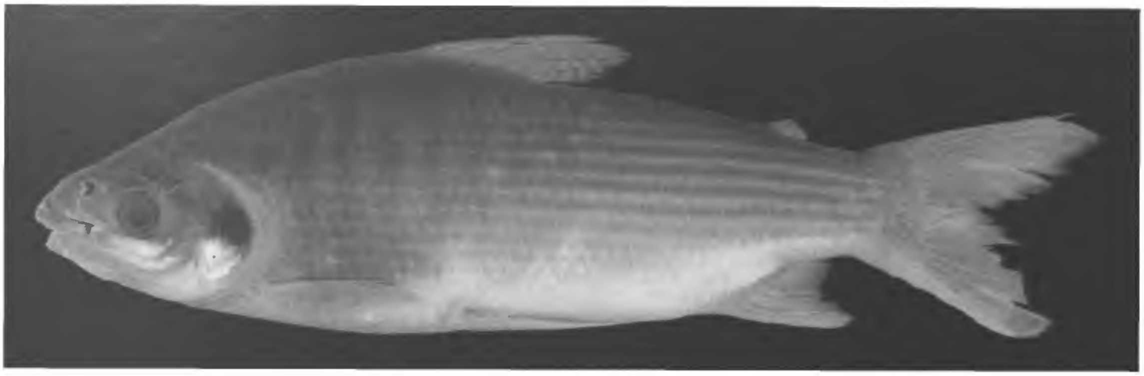


FIGURE 40.—*Prochilodus costatus,* MZUSP 21718, 227.0 mm SL; Brazil, Minas Gerais, Três Marias, Rio São Francisco.

from *P. magdalenae* in the possession of a series of wavy, dark, horizontal stripes on the lateral surface of the body (stripes absent in *P. magdalenae*), the number of vertebrae (41 to 43, 42 most frequent and 41 rare, versus 39 to 41, 41 most frequent, respectively), and to lesser degree in the number of predorsal median scales (14 to 18, 17 most frequent and 14 rare, versus 12 to 17, 14 and 15 most frequent and 17 infrequent); and from *P. lineatus* in the number of scales along the lateral line (44 to 47, 45 most frequent and 47 in only 1 of 32 specimens examined for this feature, versus 44 to 50, 47 most frequent and 44 to 46 in only 20% of specimens examined for this feature, respectively; Figure 41) and in the number of vertebrae (41 to 43, with 41 and 42 most frequent and together occurring in 92.0% of specimens examined for this feature and 43 in only one specimen, versus 42 to 44, with 43 and 44 in 85% of specimens examined for this feature, respectively; Figure 42).

DESCRIPTION.—Morphometric and meristic data for *Prochilodus costatus* presented in Table 8. Body moderately high, transversely compressed. Greatest body depth at dorsal-fin origin. Dorsal profile of head gently concave. Predorsal profile of body moderately convex. Body profile posteroventrally inclined along dorsal-fin base; gently convex from posterior of dorsal-fin base to adipose-fin origin, and concave along caudal peduncle. Predorsal portion of body with slight median

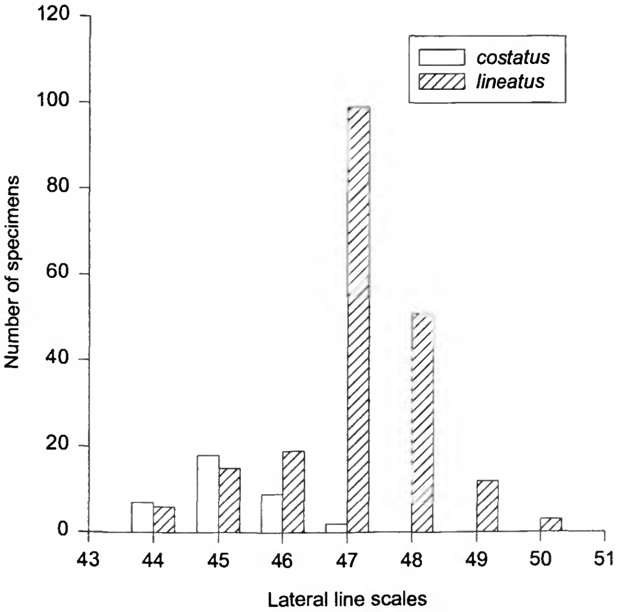


FIGURE 41.—Histogram of number of lateral-line scales plotted against number of specimens with particular counts in *Prochilodus costatus* and *Prochilodus lineatus.*

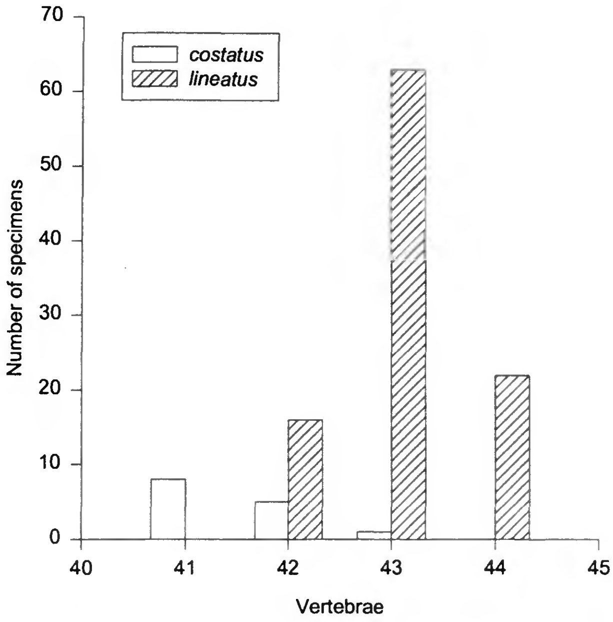


FIGURE 42.—Histogram of number of vertebrae plotted against number of specimens with particular counts in *Prochilodus costatus* and *Prochilodus lineatus.*

TABLE 8.—Morphometrics and meristics of *Prochilodus costatus:* (A) holotype of *Prochilodus costatus,* MNHN A.8636 (specimen dried and stuffed with straw); (B) lectotype of *Prochilodus affinis,* ZMUC 81; (C) paralectotypes of *Prochilodus affinis,* ZMUC 77–78; and (D) all specimens of *Prochilodus costatus* from which counts and measurements were taken (morphometric data for holotype of *Prochilodus costatus* excluded from ranges as consequence of method of preservation of that specimen; see "Remarks"). Standard length is presented in mm; values 2 to 16 are percentages of SL, 17 to 21 are percentages of HL. Dash indicates unobtainable datum, and question mark indicates specimen damaged for the indicated feature.

Characters	A	B	C	D
			Morphometrics	
1. Standard length	328.9	208.6	248.5–250.4	90.0–419.5
2. Greatest body depth	25.3	33.0	29.9–35.3	29.1–40.0
3. Predorsal length	42.5	44.5	43.0–46.7	42.4–49.5
4. Dorsal-fin base length	15.3	16.8	15.8–16.3	14.0–17.2
5. Dorsal fin to adipose fin distance	27.4	29.3	27.9–28.2	23.5–30.5
6. Dorsal fin to caudal fin distance	41.6	45.2	44.2–44.3	40.7–52.2
7. Prepelvic length	49.6	50.4	48.4–51.1	47.7–57.9
8. Preanal length	78.9	77.3	76.4–78.3	73.8–80.1
9. Snout to anal-fin insertion	83.2	81.6	80.6–82.1	79.3–85.9
10. Anal-fin base length	9.3	10.1	11.1–11.6	8.5–11.6
11. Caudal-peduncle length	12.3	14.5	12.8–13.7	11.6–14.7
12. Dorsal-fin length	12.4?	30.7	27.9–29.4	25.4–34.2
13. Pectoral-fin length	19.6	20.2	19.0–21.2	18.1–22.9
14. Pelvic-fin length	16.3?	20.1	19.6–21.7	16.3–21.7
15. Least caudal-peduncle height	9.7	12.5	12.3–13.0	11.3–14.1
16. Head length	23.7	25.7	25.4–26.0	22.2–30.7
17. Snout length	42.2	42.5	40.9–41.9	37.8–45.9
18. Bony orbital diameter	16.5	21.0	20.2–20.3	14.4–30.1
19. Postorbital length	43.2	41.9	43.4–43.5	35.7–43.5
20. Interorbital width	45.0	50.7	48.3–51.2	48.3–57.4
21. Mouth width	33.5	45.3	43.3–45.1	32.6–47.3
			Meristics	
Lateral-line scales	44	45	45–46	44–47
Scale rows between dorsal-fin origin and lateral line	9	8	9	8–9
Scale rows between anal-fin origin and lateral line	6	7	6–7	6–7
Sale rows between pelvic-fin insertion and lateral line	8	8	8	7–8
Rows of scales around caudal peduncle	17	18	18	16–18
Median predorsal scales	18	14	15	14–18
Median scales between dorsal and adipose adipose fins	18	18	16	14–18
Vertebrae	–	42	42	41–43
Inner row teeth, upper jaw	–	22	21–23	20–23
Inner row teeth, lower jaw	–	13	10–14	10–14

ridge. Postdorsal portion of body transversely obtusely rounded. Ventral profile of body gently convex from tip of lower jaw to posterior of anal-fin base. Ventral profile of caudal peduncle concave. Prepelvic region of body transversely flattened proximate to pelvic-fin insertion. Slightly developed median keel present between pelvic-fin insertion and anus.

Head profile pointed. Mouth terminal. Snout length greater than horizontal width of orbit. Nares of each side of head close to each other; anterior nares circular, posterior nares crescent shaped. Adipose eyelid present and moderately developed; most developed anteriorly but with greater part of eye uncovered. Lips fleshy but moderately developed, forming oral disk when protracted.

Functional teeth in two rows in each jaw. All teeth of similar size, with exposed portions spoon shaped except when worn down and movably implanted in flesh that overlies jaws. Inner tooth series in each jaw with 20 to 23 teeth on left side of upper jaw and 10 to 14 teeth on left side of lower jaw. Outer row of teeth in each jaw with approximately 105 teeth on each side of upper jaw and approximately 75 teeth on each side of lower jaw in lectotype of *P. affinis*. Upper and lower lips bordered by numerous globular, fleshy papillae.

Scales spinoid. Scales in middorsal series between posterior of dorsal-fin base and adipose-fin origin similar in form to those of adjoining regions of body. Lateral line with 44 to 47 (50% of specimens with 45) pored scales; 8 or 9 (73.1% of specimens with 9) horizontal rows of scales between dorsal-fin origin and lateral line; 7 or 8 (57.7% of specimens with 7) horizontal rows of scales between pelvic-fin insertion and lateral line; 6 or 7 (73.1% of specimens with 6) horizontal rows of scales between anal-fin origin and lateral line; 14 to 18 (50.0% of specimens with 17) median predorsal scales; 14 to 18

(41.7% of specimens with 15) scales in middorsal series between posterior of dorsal-fin base and adipose-fin origin; 16 to 18 (73.1% of specimens with 18) horizontal rows of scales around caudal peduncle.

Dorsal fin preceded by small, but well-developed, anteroventrally bifurcate procumbent spine somewhat triangular in lateral view. Dorsal-fin rays (including procumbent spine) iii,10 [iii,10]; anal-fin rays iii,7 or 8, or ii,7 or 8 (iii,8 most frequent) [iii,8]; pectoral-fin rays i,13 to 16 (i,14 most frequent) [i,14]; pelvic-fin rays i,7 or 8 (i,7 rare) [i,7]; principal caudal-fin rays 10/9 [10/9].

Vertebrae 41 to 43 (66.7% of specimens with 42).

Dorsal fin truncate, slightly pointed distally; posterior unbranched and anterior branched rays longest and subequal. Dorsal-fin origin located closer to tip of snout than to caudal-fin base. Greatest length of adipose fin approximately equal to horizontal width of orbit. Adipose-fin origin located along vertical that passes through posterior one-third of anal-fin base. Pectoral fin distally pointed. Tip of adpressed pectoral fin reaching posteriorly almost to pelvic-fin insertion. Pelvic fin falcate. Pelvic-fin insertion situated slightly posterior of vertical that passes through dorsal-fin origin. Tip of adpressed pelvic fin reaching approximately four-fifths of distance between pelvic-fin insertion and anus. Axillary scale present, its length approximately one-third of pelvic-fin length. Posterior unbranched and anterior branched anal-fin rays longest and subequal. Caudal-fin margin gently bifurcate.

COLORATION IN ALCOHOL.—Ground coloration silvery yellow or brownish yellow, with dorsal portions of body and head darker. Lateral surface of body with 7 to 15 (most frequently 12) dark, vertical patches of irregular form located between head and caudal fin. Patches with overall form of approximately narrow isosceles triangles with apexes located on middle of ventrolateral portion of body and bases along dorsomedial region. Patches well developed in smaller specimens but indistinct or absent in larger individuals. Lateral surface of body with approximately 6 to 12 dark, wavy, horizontal stripes along dorsal and ventral margins of exposed portions of scales. Approximately 4 to 6 (most frequently 5) wavy stripes above lateral line and approximately 2 to 6 (most frequently 4) wavy stripes below. Field of black or brown chromatophores forming dark mark of irregular form on upper one-half of opercle.

Dorsal fin with 4 to 8 (most frequently 6) dark, irregular stripes beginning on anterior margin of fin and extending across fin approximately parallel to fin base. Adipose fin with dorsal margin finely bordered with black. Pectoral, pelvic, anal, and caudal fins dusky. Iris orangish brown, with areas of diffuse dusky pigmentation dorsally and ventrally.

COLORATION IN LIFE.—(Based upon a photograph of recently deceased specimen from the upper portions of the Rio São Francisco basin taken by the senior author. Same photograph was reproduced in Casatti and Castro (1998, fig. 4d)). Dark coloration as in preserved specimens. Ventrolateral portion of body reddish. Similar reddish coloration present on pelvic fin, particularly anteriorly, and on anal fin.

DISTRIBUTION.—*Prochilodus costatus* was originally endemic to, and widely distributed throughout, the Rio São Francisco basin, eastern Brazil (Figure 43, stars). Godinho et al. (1999:423) reported that *P. costatus* has been introduced into the Rio Jequitinhonha basin of eastern Brazil.

COMMON NAME.—Curimatá, curimatã-pioa, curimatá-pioa (Brazil).

COMPARISONS.—*Prochilodus costatus* unequivocally differs from each of its congeners, with the exception of *P. lineatus,* in at least one meristic or pigmentary feature. *Prochilodus costatus* and *P. lineatus,* although occurring in river systems whose headwaters lie in proximity (Rio São Francisco and Río de La Plata basins, respectively), demonstrate a strong modal difference in the number of lateral line scales and, to a lesser degree, a difference in the number of vertebrae (Figures 41–43) and are, thus, recognized herein as distinct species.

REMARKS.—Valenciennes' (1850:79–80) description of *Prochilodus costatus* was based upon the holotype (MNHN A.8636) collected by Saint-Hilaire in the Rio São Francisco, Minas Gerais, Brazil (see Papavero, 1971, map 10, for itinerary of that collecting expedition). *Prochilodus costatus* and *P. argenteus* are endemic to the Rio São Francisco, Brazil, and the two species have been misidentified as each other by various authors (see synonymy); these errors have resulted in confusion in the literature as to the actual distributions of the two taxa. The two species can, however, be discriminated by the number of horizontal rows of scales between the lateral line and the dorsal-fin origin.

Lütken (1875a:128; 1875b:189–193, fig. 69) described *Prochilodus affinis* from three specimens collected by Reinhardt in the Rio das Velhas, Minas Gerais, Brazil. As shown in Table 8, no differences were found in this study that serve to discriminate *P. affinis* from *P. costatus*; therefore, we place *P. affinis* as a junior synonym of *P. costatus,* and all citations of *P. affinis* from the Rio São Francisco are considered to refer to *P. costatus*. We herein designate ZMUC 81 (208.6 mm SL), the specimen that is in the best overall condition of the syntypes, as the lectotype of *Prochilodus affinis,* and the two other syntypes (ZMUC 77, 248.5 mm SL; ZMUC 78, 250.4 mm SL) consequently become paralectotypes.

Until this publication, *Prochilodus brevis* was not known to be present in the Rio São Francisco system and even now is only known from a limited area to the north of the lower portion of that river basin. Given that situation, it seems likely that the citation of *P. brevis* from that river basin by Nomura (1984:54) most likely refers, at least in part, to *P. costatus*. *Prochilodus steindachneri* (=*Prochilodus vimboides*) was erroneously cited by Fowler (1941:171) from the Rio São Francisco, perhaps accounting for the subsequent erroneous citation by Nomura (1984:54) of that species from that river system.

Prochilodus reticulatus is endemic to Lago Maracaibo in northwestern South America, an area far distant from the Rio

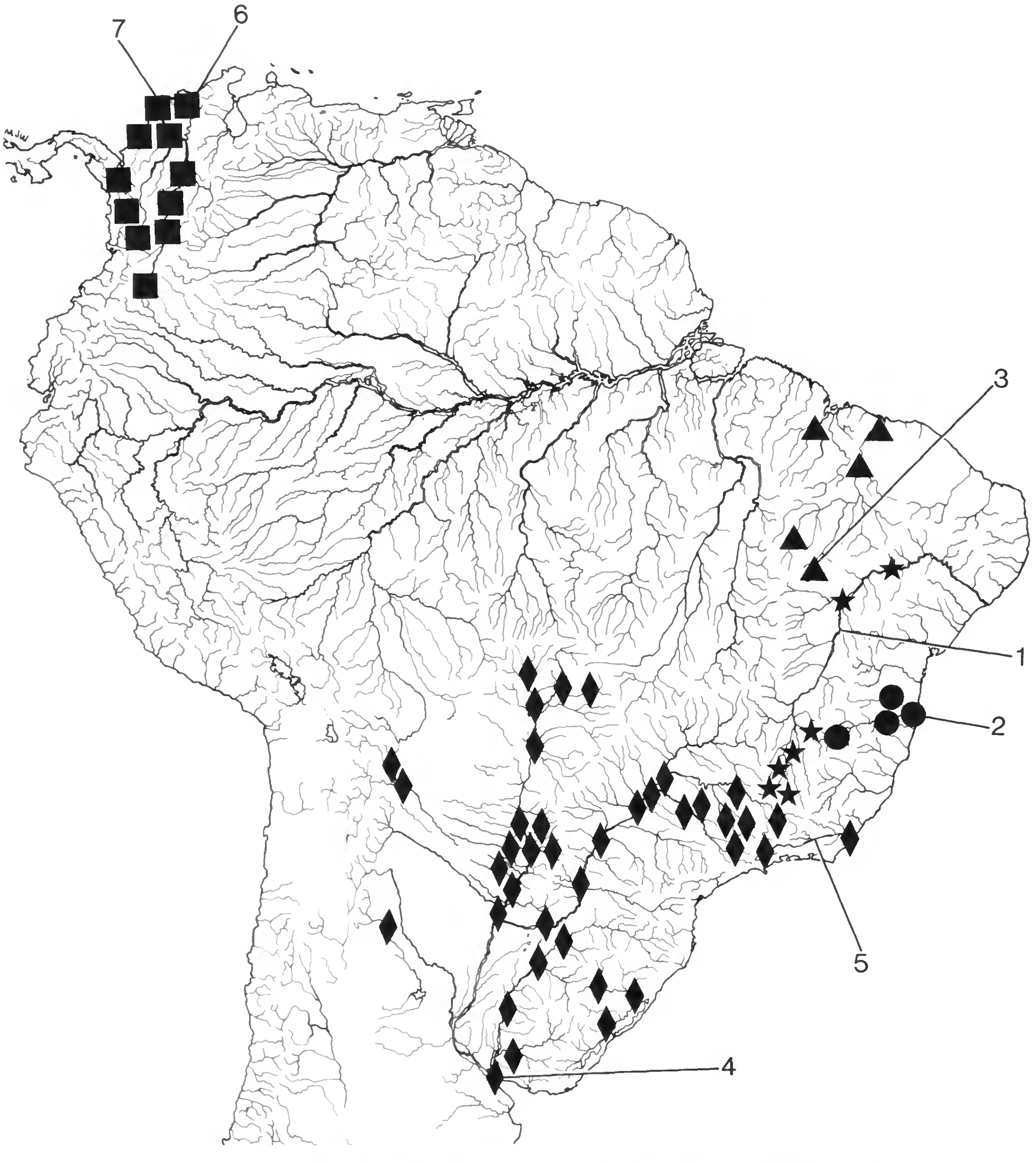


FIGURE 43.—Map of central and northern South America showing geographic distribution of *Prochilodus costatus* (stars; 1=Rio São Francisco, inexact type locality), *Prochilodus hartii* (dots; 2=lectotype locality), *Prochilodus lacustris* (triangles; 3=lectotype locality), *Prochilodus lineatus* (diamonds; 4=type locality of *Pacu* (= *Prochilodus*) *lineatus* and *Prochilodus platensis;* 5=Rio Paraíba do Sul, inexact type locality of *Prochilodus scrofa*), and *Prochilodus magdalenae* (squares; 6=lectotype locality of *Prochilodus magdalenae* and approximate type locality of *Prochilodus eigenmanni;* 7=type locality of *Prochilodus beani*) (some symbols represent more than one collecting locality and/or lot of specimens).

São Francisco basin of eastern South America. The citation of *P. reticulatus* by Pearson (1937b:109) for the Rio São Francisco is consequently incorrect and perhaps refers to *P. costatus*, a species of somewhat similar overall appearance.

MATERIAL EXAMINED.—43 specimens (26, 90.0–419.5 mm SL).

BRAZIL. *Bahia:* Barra, Rio São Francisco, NMW 9585, 1 (1, 264.0). Rio São Francisco, close to Barragem de Sobradinho, MZUSP 21549, 2 (2, 237.0–252.0). Rio São Francisco, MZUSP 3797, 3 (3, 105.0–116.6). *Minas Gerais:* Rio das Velhas, approximately 32 miles (51.2 km) N of Belo Horizonte, BMNH 1925.6.9:1, 1 (1, 419.5). Rio das Velhas, BMNH 1876.1.10:26, 1 (1, 220.2) [1R]. Rio das Velhas, ZMUC 81, 1 (1, 208.6, lectotype of *Prochilodus affinis*) [1R]. Ribeirão do Mato (locality approximately 24 km N of Belo Horizonte), ZMUC 77, 1 (1, 248.5, paralectotype of *Prochilodus affinis*) [1R]; ZMUC 78, 1 (1, 250.4, paralectotype of *Prochilodus affinis*) [1R]. Rio São Francisco, MNHN A.8636, 1 (1, 328.9, holotype of *Prochilodus costatus*). Rio São Francisco, upper portion (20°30′S, 46°50′W), MZUSP 50740, 1 (315.5). Três Marias, Rio São Francisco, MZUSP 20818, 5 (5, 90.0–114.0); MZUSP 21452, 1 (1, 265.0); MZUSP 21718, 5 (5, 170.0–302.0). Pirapora, Rio São Francisco, CAS 59319, 1 (155.5); MZUSP 2081, 3 (3, 135.0–203.0). Rio São Francisco, Pontal do Abaeté, projeto Usina Hidrelétrica Formoso, MZUSP 39699, 3 (214.0–246.3). Rio São Francisco and tributaries, area of projeto Usina Hidrelétrica Formoso, MZUSP 39739, 6 (212.8–258.3). Riacho tributary to Rio Jequitaí, along highway BR-135, between Buenópolis and Engenheiro Dolabela (latter locality at 17°30′S, 44°05′W), USNM 357391, 2 (101.6–105.1). Montes Claros, Rio Verde, between Montes Claros and Francisco Sá (16°28′S, 43°30′W), USNM 345876, 3 (93.1–192.9). Porteirinha, Rio Serra Branca, tributary of Rio Salinas, along highway BR-122, between Mato Verde and Porteirinha (latter locality at 15°44′S, 43°02′W), USNM 345755, 1 (126.3).

Prochilodus hartii Steindachner, 1874

FIGURES 43, 44; TABLE 9

Prochilodus hartii Steindachner, 1874:533, pl. 5 [type locality: Rio Jequitinhonha, Rio Pardo und Rio Parahyba (=Brazil, Rio Jequitinhonha, Rio Pardo, and Rio Paraíba do Sul), restricted herein to Brazil, Bahia, Rio Jequitinhonha, Belmonte].—Cope, 1878:685 [contrasted with *P. hartii*].—Eigenmann and Eigenmann, 1891:48 [in listing of South American fishes].—Eigenmann, 1907b:768 [lateral-line scale count]; 1910:424 [in listing of South American fishes].—Magalhães, 1931:111 [in part, not synonymy into *Prochilodus reticulatus*].—Fowler, 1941:171 [brief redescription]; 1950:218 [literature compilation in part; not cited occurrence in Rio Paraíba do Sul]; 1975:359 [Brazil, Rio Jequitinhonha and Bardo (= Pardo), not cited occurrence in Rio Parahyba (=Paraíba)].—Mago-Leccia, 1972:47 [use of caudal-fin pigmentation to group species].—[Not Fowler, 1950:218 (citation for São Paulo); Géry, 1977:219 [(Brazil), Rio Parahyba (= Paraíba)].

Prochilodus cf. *hartii*.—Godinho et al., 1999:415, 418, 421, tables 18.1, 18.2, / 18.4 [Brazil, Rio Jequitinhonha; common name; habitat; biological information].

DIAGNOSIS.—*Prochilodus hartii* differs from *P. brevis, P. lacustris, P. mariae, P. nigricans,* and *P. rubrotaeniatus* in its lack of dark, irregular, wavy, bar-like patterns on the caudal-fin lobes that are present in those five species. Within the group of *Prochilodus* species with hyaline caudal fins, *P. hartii* differs from *P. vimboides* in the number of lateral-line scales (40 to 43, 41 most frequent, versus 34 to 39, 37 most frequent, respectively); from *Prochilodus britskii* in the number of teeth in the inner tooth row on each side of the upper jaw (21 to 28 versus 10 to 13, respectively) and in the number of teeth in the inner tooth series of each side of the lower jaw (13 to 18 versus 6 or 7, respectively); from *P. argenteus, P. costatus,* and *P. lineatus* in the number of scales along the lateral line (40 to 43, 41 most frequent, versus the range of 44 to 51 in these three species in combination); from *P. reticulatus* in the number of teeth in the inner row of teeth in the lower jaw (13 to 18, 14 most frequent, versus 8 to 12, 10 most frequent, respectively) and in the number of horizontal rows of scales around the caudal peduncle (14 to 16, 14 and 15 most frequent, versus 16 to 18, 18 most frequent, respectively); and from *P. magdalenae* in the number of horizontal rows of scales around the caudal peduncle (14 to 16, 14 and 15 most frequent, versus 17 to 19, 18 most frequent, respectively) and in the number of scales along the lateral line (40 to 43, 41 most frequent, versus 43 to 46, 44 most frequent).

DESCRIPTION.—Morphometric and meristic data for *Prochilodus hartii* presented in Table 9. Body comparatively high, transversely compressed. Greatest body depth at dorsal-fin origin. Dorsal profile of head gently concave. Predorsal profile of body convex; posteroventrally inclined along dorsal-fin base; gently convex from posterior of dorsal-fin base to adipose-fin origin, and concave along caudal peduncle. Predorsal portion of body with slight median ridge. Postdorsal region of body obtusely rounded transversely. Ventral profile of body convex from tip of lower jaw to posterior of anal-fin base. Ventral profile of caudal peduncle concave. Prepelvic region transversely flattened proximate to pelvic-fin insertion. Moderately developed median keel present between pelvic-fin insertion and anus.

Head profile pointed. Mouth terminal. Snout length greater than horizontal width of orbit. Nares of each side of head close to each other; anterior nares circular, posterior nares crescent shaped. Adipose eyelid present but poorly developed; most developed anteriorly, but with greater part of eye uncovered. Lips fleshy, moderately developed, and forming oral disk when protracted.

Functional teeth in two rows in each jaw. All teeth movably implanted in flesh that overlies jaws. All teeth of similar size, with exposed portions spoon shaped except when worn down. Inner tooth series in each jaw with 21 to 28 teeth on left side of upper jaw and 13 to 18 teeth on left side of lower jaw. Outer row of teeth in each jaw with approximately 132 teeth on each side of upper jaw and approximately 100 teeth on each side of lower jaw in lectotype. Upper and lower lips bordered by numerous globular, fleshy papillae.

TABLE 9.—Morphometrics and meristics of *Prochilodus hartii:* (A) lectotype of *Prochilodus hartii,* NMW 56645; (B) paralectotypes of *Prochilodus hartii,* NMW 56646:1–4, NMW 56647, and NMW 56648; and (C) all specimens of *Prochilodus hartii* from which counts and measurements were taken. Standard length is presented in mm; values 2 to 16 are percentages of SL, 17 to 21 are percentages of HL.

Characters	A	B	C
		Morphometrics	
1. Standard length	259.5	121.2–333.8	91.6–333.8
2. Greatest body depth	34.9	30.2–35.1	30.2–39.7
3. Predorsal length	46.6	42.5–46.1	41.6–49.5
4. Dorsal-fin base length	16.8	15.9–18.0	15.9–18.0
5. Dorsal fin to adipose fin distance	27.6	28.5–30.7	24.1–31.4
6. Dorsal fin to caudal fin distance	42.5	43.1–45.4	40.1–49.7
7. Prepelvic length	51.8	48.6–51.4	48.6–56.2
8. Preanal distance	78.1	72.4–79.2	71.6–80.6
9. Snout to anal-fin insertion	81.5	77.8–82.8	75.3–83.5
10. Anal-fin base length	12.0	10.0–12.6	9.1–12.6
11. Caudal-peduncle length	12.8	11.8–14.6	11.4–14.7
12. Dorsal-fin length	28.4	26.6–31.5	24.6–32.6
13. Pectoral-fin length	21.6	20.7–22.4	17.1–23.0
14. Pelvic-fin length	19.3	19.0–20.3	17.7–22.0
15. Least caudal-peduncle height	11.2	10.5–12.2	10.5–12.5
16. Head length	25.7	24.1–26.7	24.1–28.4
17. Snout length	42.4	37.4–44.0	37.0–47.2
18. Bony orbital diameter	18.9	17.2–27.8	15.8–30.0
19. Postorbital length	39.0	36.8–43.7	35.6–43.7
20. Interorbital width	50.8	47.7–54.2	47.7–54.4
21. Mouth width	34.8	39.1–45.5	34.8–46.6
		Meristics	
Lateral-line scales	41	41–43	40–43
Scale rows between dorsal-fin origin and lateral line	7	7	6–8
Scale rows between anal-fin origin and lateral line	5	5	5–6
Scale rows between pelvic-fin insertion and lateral line	6	6	5–7
Rows of scales around caudal peduncle	14	14–15	14–16
Median predorsal scales	13	14–15	12–16
Median scales between dorsal and adipose fins	15	13–15	12–15
Vertebrae	39	39–40	37–40
Inner row teeth, upper jaw	22	22–28	21–28
Inner row teeth, lower jaw	14	14–16	13–18

Scales spinoid. Scales in middorsal series between posterior of dorsal-fin base and adipose-fin origin similar in form to those of adjoining regions of body. Lateral line with 40 to 43 (46.7% of specimens with 41) pored scales; 6 to 8 (85.7% of specimens with 7) horizontal rows of scales between dorsal-fin origin and lateral line; 5 to 7 (86.7% of specimens with 6) horizontal rows of scales between pelvic-fin insertion and lateral line; 5 or 6 (86.7% of specimens with 5) horizontal rows of scales between anal-fin origin and lateral line; 12 to 16 (50.0% of specimens with 14) median predorsal scales; 12 to 15 (43.3% of specimens with 14) scales in middorsal series between posterior of dorsal-fin base and adipose-fin origin; 14 to 16 (46.7% of specimens with 14 and 15) horizontal rows of scales around caudal peduncle.

Dorsal fin preceded by small, but well-developed, anteriorly bifurcate, procumbent spine. Dorsal-fin rays (including procumbent spine) iii,10 [iii,10]; anal-fin rays iii,8 or 9 (iii,8 most frequent) [iii,8]; pectoral-fin rays i,13 to 15 (i,14 most frequent) [i,14]; pelvic-fin rays i,8 or 9 (i,8 most frequent) [i,8]; principal caudal-fin rays 10/9 [10/9].

Vertebrae 37 to 40 (66.7% of specimens with 40).

Dorsal fin truncate, slightly pointed distally; posterior unbranched and anterior branched longest and subequal. Dorsal-fin origin located closer to tip of snout than to caudal-fin base. Greatest length of adipose fin approximately equal to horizontal width of orbit. Adipose-fin origin located along vertical that passes through middle of anal-fin base. Pectoral fin distally pointed. Tip of adpressed pectoral fin reaching posteriorly approximately three-fourths of distance between pectoral-fin and pelvic-fin insertions. Pelvic fin falcate. Pelvic-fin insertion located along vertical that passes through middle of dorsal-fin base. Tip of adpressed pelvic fin reaching posteriorly approximately two-thirds of distance between pelvic-fin insertion and anus. Axillary scale present, its length approximately one-third of greatest length of pelvic fin. Posterior unbranched and anterior branched anal-fin rays longest and subequal. Caudal fin bifurcate.

COLORATION IN ALCOHOL.—Ground coloration silvery yellow or brownish yellow, with dorsal portion of body and head darker. Lateral surface of body typically uniformly pigmented and lacking vertical patches of dark pigmentation; rarely with approximately 15 diffuse and irregular, dark, vertical patches of pigmentation between head and caudal-fin base. Pigmentation patches formed of alternating fields of highly irregular and diffuse melanophores. Small and medium-sized individuals with 7 to 10 (most frequently 8 or 9) dark, wavy, horizontal stripes along dorsal and ventral margins of exposed portions of scales. Three to 5 (most frequently 4 or 5) wavy stripes above lateral line and 3 to 4 (most frequently 4 or 5) wavy stripes below. Field of black chromatophores forming dark mark of irregular shape on upper one-half of opercle. Largest examined specimens without wavy stripes apparent on lateral surface of body, perhaps as consequence of layer of guanine that overlies that region.

Dorsal fin with 5 to 10 (most frequently 5) irregular, dark stripes beginning at anterior margin and extending across fin approximately parallel to base of fin. Adipose fin with dorsal margin finely bordered by black pigmentation. Pectoral, pelvic, anal, and caudal fins dusky. Iris yellowish gold, with diffuse, dusky areas on dorsal and ventral portions.

COLORATION IN LIFE.—(Based upon color transparencies of recently collected specimens from the Rio Jequitinhonha photographed by the first author). Dark pigmentation as described above. Ground coloration silvery, with dorsal portion of head and body darker, especially the head. All fins with reddish ground coloration, with posterior portions of pelvic and anal fins more intensely red and with interradial membranes of anal fin and all of caudal fin somewhat dusky. Iris golden yellow.

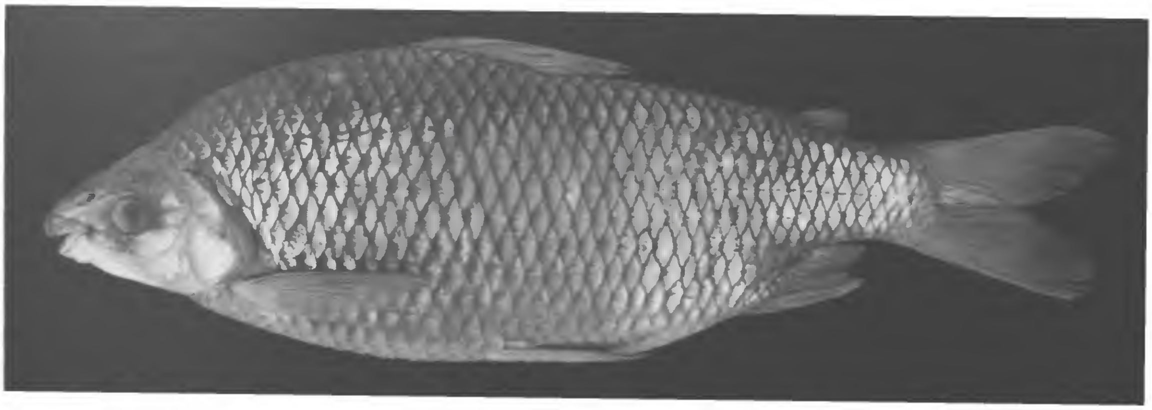


FIGURE 44.—*Prochilodus hartii*, NMW 56647, 333.8 mm SL; Brazil, Bahia, Canavieiras, Rio Pardo.

DISTRIBUTION.—*Prochilodus hartii* is known only from the Rio Pardo and Rio Jequitinhonha basins of eastern Brazil (Figure 43, dots).

COMMON NAME.—Grumexa or grumecha, curimatã, papaterra (Brazil).

COMPARISONS.—As noted in the "Diagnosis," *Prochilodus hartii* is unequivocally distinguished from all congeners by various meristic, morphometric, and pigmentary features.

REMARKS.—Steindachner (1874:533–536, pl. 5) described *Prochilodus hartii* from specimens that originated in the Rio Jequitinhonha and Rio Pardo basins of eastern Brazil and that were most likely collected by Hartt and Copeland during the Thayer Expedition. As such, these specimens were presumably originally deposited at the MCZ and taken back to Vienna by Steindachner after his visit to the MCZ. Steindachner did not designate a holotype for *P. hartii,* but seven syntypes of the species have been located in the Naturhistorisches Museum Wien (NMW). We herein designate NMW 56645 (259.5 mm SL), the syntype in the best overall condition, and that originated in the Rio Jequitinhonha, as the lectotype of *P. hartii.* The other syntypes collected at the same locality (NMW 56646:1–4, 121.2–235.7 mm SL; NMW 56648, 245.8 mm SL) thus become paralectotypes, as does the single syntype (NMW 56647, 333.8 mm SL) from the Rio Pardo at Canavieiras, Bahia.

Notwithstanding Steindachner's (1874:536) report of *Prochilodus hartii* from the Rio Parahyba [= Paraíba] in southeastern Brazil, we failed to encounter any specimens of the species in the examined ichthyofaunal samples from that basin. Rather, all examined specimens of *P. hartii,* including those collected by the first author and collaborators in the coastal rivers of eastern Brazil, originated in the Rios Pardo and Jequitinhonha. Thus, it appears that the citation by Steindachner (1874:536) of *P. hartii* from the Rio Paraíba (Rio Paraíba do Sul) is erroneous and is likely a misidentification of a lot of *Prochilodus vimboides,* a species that is a component of the Rio Paraíba do Sul ichthyofauna and that is quite similar in overall appearance, meristics, and morphometrics to *P. hartii.*

MATERIAL EXAMINED.—43 specimens (30, 91.6–333.8 mm SL).

BRAZIL. *Bahia:* Rio Jequitinhonha, Belmonte, MCZ 20042, 3 (1, 125.6–136.6); MCZ 20043, 2 (2, 293.1–303.7) [1R]; MCZ 20044, 2 (2, 128.7–156.0) [1R]; MZUSP 2799, 10 (10, 91.6–124.0); MZUSP 42685, 2 (cleared and counterstained for bone and cartilage); NMW 56645, 1 (1, 259.5, lectotype of *Prochilodus hartii*) [1R]; NMW 56646:1–4, 4 (4, 121.2–235.7, paralectotypes of *Prochilodus hartii*) [4R]; NMW 56648, 1 (1, 245.8, paralectotype of *Prochilodus hartii*) [1R]. Rio Pardo, Canavieiras, MCZ 20047, 2 (1, 189.0–195.3); NMW 56647, 1 (1, 333.8, paralectotype of *Prochilodus hartii*) [1R]. Rio Pardo, near Itapetininga, MZUSP 42676, 1 (1, 173.4) [1R]. *Minas Gerais:* Rio Jequitinhonha, Salto da Divisa, MZUSP 42677, 3 (3, 244.8–300.0) [3R]; USNM 319769, 1 (270.2) [1R]. Rio Araçuaí, MCZ 20045, 3 (1, 210.2) [1R]; MCZ 20159, 2 (1, 122.4–128.8). Rio Ribeirão, tributary of Rio Jequitinhonha, approximately 4–5 km ESE of Jordania (15°54'S, 40°10'W), USNM 318129, 3 (86.7–91.8); USNM 318135, 2 (94.1–100.9).

***Prochilodus lacustris* Steindachner, 1907**

FIGURES 43, 45; TABLE 10

Prochilodus lacustris Steindachner, 1907:152 (page 1 of separate) [type locality: See von Parnagua unde der nahegelegenen, Lagoa da Missão; Lagoas bei Sa. Filomena und am Rio Medonho einem Nebenflusse des Parnahyba (= Brazil, Piauí, Lagoa de Parnaguá, Lagoa da Missão, Santa Filomena and Rio Medonho, tributary to Rio Parnaíba), restricted herein to Brazil, Piauí, Lago de Parnaguá, Rio Gurguéia system].—Eigenmann, 1910:424 [in listing of South American fishes].—Fowler, 1950:220 [literature compilation]; 1975: 359 [literature compilation; common name].—Mago-Leccia, 1972:47 [use of caudal-fin pigmentation to discriminate groups of species].—Nomura, 1984: 54 [Brazil, common name].—Petrere, 1989:8 [economic importance].

Prochilodus argenteus [not of Agassiz, 1829].—Steindachner, 1915:21 [in part, incorrect synonymy of *P. lacustris* into *P. argenteus*].—Géry, 1977:222 [in part; not *P. lacustris* as synonym of *P. argenteus*].—Nomura, 1984:54 [Brazil, common name].

Prochilodus nigricans [not of Agassiz, 1829].—Nomura, 1984:54 [Brazil, common name].

FIGURE 45.—*Prochilodus lacustris*, MZUSP 5064, 111.0 mm SL; Brazil, Maranhão, Rio Grajaú.

DIAGNOSIS.—The pattern of dark, irregular, wavy, bar-like patterns on the caudal-fin lobes in *Prochilodus lacustris* discriminates that species from *P. argenteus, P. britskii, P. costatus, P. hartii, P. lineatus, P. magdalenae, P. reticulatus,* and *P. vimboides,* which have hyaline caudal fins. Within the group of five *Prochilodus* species with dark, irregular caudal-fin bars, *P. lacustris* differs from *P. mariae* in the number of scales along the lateral line (46 to 51, 47 most frequent with 51 in 2 of the 50 specimens examined for this feature, versus 52 to 64, 52 in only 1 of the 77 specimens examined for this feature, respectively), the number of scales along the middorsal series between the posterior of the dorsal-fin base and the adipose-fin origin (14 to 18, 16 most frequent, versus 17 to 23, 18 and 19 most frequent, respectively), and the number of dark, wavy, horizontal stripes ventral of the lateral line (6 or 7 versus 7 to 10, respectively); from *P. brevis* in the number of horizontal rows of scales between the pelvic-fin insertion and the lateral line (8 to 11, with 9 most frequent and 8 infrequent, versus 6 to 8, with 7 most frequent and 8 infrequent, respectively; Figure 36), the number of scales along the lateral line (46 to 51, 47 most frequent and 46 in only 17% of examined specimens, versus 41 to 48, 43 most frequent and 46 to 48 infrequent, respectively; Figure 37), and the number of vertebrae (41 to 43, with 42 most frequent and 41 in only 1 of 13 specimens examined for this feature, versus 40 to 42, with 42 and 41 most frequent and 42 in only 2 of 30 specimens examined for this feature, respectively; Figure 38); from *P. rubrotaeniatus* in the form of the scales (with only radial subdivisions versus having complex pattern of variable subdivisions), the number of horizontal rows of scales between pelvic-fin insertion and lateral line (8 to 11, 9 most frequent and 8 in only 8 of 51 specimens, versus 6 to 8, 6 most frequent and 8 in only 2 of 36 specimens, respectively); from *P. nigricans* in the form of the scales (with only radial subdivisions versus having complex pattern of variable subdivisions), the number of scales along the lateral line (46 to 51, 47 most frequent, versus 44 to 51, 49 most frequent, respectively), the number of horizontal rows of scales between the pelvic-fin insertion and the lateral line (8 to 11, 9 most frequent, versus 7 to 9, 8 most frequent, respectively), the number of median predorsal scales (15 to 22, 16 most frequent, versus 13 to 20, 17 most frequent, respectively), and the number of vertebrae (41 to 43, 42 most frequent, versus 40 to 45, 43 most frequent).

DESCRIPTION.—Morphometric and meristic data for *Prochilodus lacustris* presented in Table 10. Body comparatively high, transversely compressed. Greatest body depth at dorsal-fin origin. Dorsal profile of head gently concave. Predorsal profile of body convex. Body profile posteroventrally inclined along dorsal-fin base, straight from posterior of dorsal-fin base to adipose-fin origin, and concave along caudal peduncle. Predorsal portion of body with moderately developed median ridge. Postdorsal region of body transversely obtusely rounded. Ventral profile of body convex from tip of lower jaw to posterior of anal-fin base. Ventral profile of caudal peduncle concave. Prepelvic region transversely flattened proximate to pelvic-fin insertion. Distinct median keel present between pelvic-fin insertion and anus.

Head profile pointed. Mouth terminal. Snout length greater than horizontal width of orbit. Nares of each side of head close to each other; anterior nares circular, posterior nares crescent shaped. Adipose eyelid present but only slightly developed anteriorly, and with major part of eye uncovered. Lips fleshy, moderately developed, and forming oral disk when protracted.

Functional teeth in two rows in each jaw. All teeth movably implanted in flesh that overlies jaws. All teeth of similar size, with exposed portion spoon shaped except when worn down.

TABLE 10.—Morphometrics and meristics of *Prochilodus lacustris:* (A) lectotype of *Prochilodus lacustris,* NMW 56674:4; (B) paralectotypes of *Prochilodus lacustris,* NMW 56674:1–3 and NMW 56674:5; and (C) all specimens of *Prochilodus lacustris* from which counts and measurements were taken. Standard length is presented in mm; values 2 to 16 are percentages of SL, 17 to 21 are percentages of HL.

Characters	A	B	C
		Morphometrics	
1. Standard length	124.6	85.0–123.1	57.2–324.3
2. Greatest body depth	41.3	37.3–43.3	31.8–49.7
3. Predorsal length	47.8	47.2–48.7	44.0–48.7
4. Dorsal-fin base length	17.7	16.9–17.8	15.6–19.5
5. Dorsal fin to adipose fin distance	24.5	24.5–26.5	21.0–28.0
6. Dorsal fin to caudal fin distance	41.9	41.6–43.4	39.0–48.3
7. Prepelvic length	55.3	52.6–53.6	49.1–57.1
8. Preanal distance	77.9	76.5–78.6	71.0–81.0
9. Snout to anal-fin insertion	81.9	80.5–83.1	72.9–84.0
10. Anal-fin base length	12.2	10.8–12.9	10.3–12.9
11. Caudal-peduncle length	13.4	13.2–13.7	11.7–14.8
12. Dorsal-fin length	32.7	30.4–32.5	22.9–34.1
13. Pectoral-fin length	20.5	21.3–22.2	13.5–22.8
14. Pelvic-fin length	19.9	19.8–21.5	12.9–21.5
15. Least caudal-peduncle height	12.6	11.9–12.6	10.3–13.3
16. Head length	28.6	29.9–30.1	24.8–34.4
17. Snout length	38.5	36.0–37.8	33.0–50.0
18. Bony orbital diameter	27.5	25.5–28.1	20.0–36.5
19. Postorbital length	39.0	37.0–40.3	32.5–44.6
20. Interorbital width	56.2	54.3–57.0	52.4–63.5
21. Mouth width	46.9	43.8–47.6	37.1–57.1
		Meristics	
Lateral-line scales	49	47–49	46–51
Scale rows between dorsal-fin origin and lateral line	10	10–11	9–13
Scale rows between anal-fin origin and lateral line	8	7–9	7–9
Scale rows between pelvic-fin insertion and lateral line	10	9–10	8–11
Rows of scales around caudal peduncle	22	19–22	16–25
Median predorsal scales	17	17–22	15–22
Median scales between dorsal and adipose fins	16	15–17	14–18
Vertebrae	42	42	41–43
Inner row teeth, upper jaw	15	16–17	13–20
Inner row teeth, lower jaw	9	7–10	7–10

Inner tooth series in each jaw with 13 to 20 teeth on left side of upper jaw and 7 to 10 teeth on left side of lower jaw. Outer row of teeth in each jaw with approximately 78 teeth on each side of upper jaw and approximately 75 teeth on each side of lower jaw in lectotype. Upper and lower lips bordered by numerous globular, fleshy papillae.

Scales spinoid. Scales in middorsal series between posterior of dorsal-fin base and adipose-fin origin similar in form to those of adjoining regions of body. Lateral line with 46 to 51 (42.9% of specimens with 47) pored scales; 9 to 13 (42.0% of specimens with 10) horizontal rows of scales between dorsal-fin origin and lateral line; 8 to 11 (49.0% of specimens with 9) horizontal rows of scales between pelvic-fin insertion and lateral line; 7 to 9 (60.0% of specimens with 8) horizontal rows of scales between anal-fin origin and lateral line; 15 to 22 (32.7% of specimens with 16) median predorsal scales; 14 to 18 (33.3% of specimens with 16) scales in middorsal series between posterior of dorsal-fin base and adipose-fin origin; 16 to 25 (24.5% of specimens with 22) horizontal rows of scales around caudal peduncle.

Dorsal fin preceded by small, but well-developed, anteroventrally bifurcate, procumbent spine somewhat triangular in lateral view. Dorsal-fin rays (including procumbent spine) iii,10 [iii,10]; anal-fin rays iii,8 or 9, or ii,8 or 9 (iii,8 most frequent) [iii,8]; pectoral-fin rays i,13 to 16 (i,14 most frequent) [i,14]; pelvic-fin rays i,7 to 9 (i,8 most frequent) [i,8]; principal caudal-fin rays 10/9 [10/9].

Vertebrae 41 to 43 (72.7% of specimens with 42).

Dorsal fin truncate and gently pointed distally; posterior unbranched and anterior branched rays longest and subequal. Dorsal-fin origin located closer to tip of snout than to caudal-fin base. Greatest length of adipose fin approximately four-fifths of horizontal width of orbit. Adipose-fin origin located along vertical that passes through posterior one-third of anal-fin base. Pectoral fin distally pointed. Tip of adpressed pectoral fin extending posteriorly to, or almost to, pelvic-fin insertion. Pelvic fin falcate. Pelvic-fin insertion located along vertical that passes through posterior one-third of dorsal-fin base. Tip of adpressed pelvic fin extending posteriorly approximately four-fifths of distance between pelvic-origin insertion and anus. Axillary scale present, its length approximately one-third of greatest length of pelvic fin. Posterior unbranched and anterior branched anal-fin rays longest and subequal. Caudal fin moderately bifurcate.

COLORATION IN ALCOHOL.—Ground coloration silvery yellow or brownish yellow, with dorsal portion of body and head darker. Lateral surface of body with approximately 8 to 18 (most frequently 13) dark, irregular, diffuse patches between head and caudal fin; patches with overall approximate form of narrow isosceles triangles, with apexes positioned in middle of ventrolateral portion of body and bases on dorsomedial region of body. Patches well developed in small specimens but indistinct or absent in large individuals. Lateral surface of body with approximately 13 to 18 (most frequently 14) dark, wavy, horizontal stripes along dorsal and ventral margins of exposed portions of scales. Approximately 5 to 8 (most frequently 5) dark, wavy stripes above lateral line, and 7 to 10 (most frequently 8) dark, wavy stripes below. Field of black and brown chromatophores forming dark mark of irregular shape on upper one-half of opercle.

Dorsal fin with 5 or 6 (most frequently 5) dark, irregular stripes starting along anterior margin and extending across fin approximately parallel to fin base. Adipose fin with small dark marks and dorsal border dusky. Pectoral, pelvic, and anal fins hyaline to dusky. Caudal fin with 2 to 5 (most frequently 3) [4] irregular or wavy, vertical bars formed by groups of dark chromatophores. Iris yellowish silver, with diffuse dusky areas on dorsal and ventral portions.

Distribution.—*Prochilodus lacustris* is only known from the Rio Mearim and Rio Parnaíba basins, northeastern Brazil (Figure 43, triangles).

Common Name.—Curimatã (Brazil).

Comparisons.—The combination of the presence of distinct, dark, caudal-fin pigmentation, the possession of cruciform but not elaborate subdivisions of the scales, and various meristic and morphometric features unequivocally distinguish *Prochilodus lacustris* from all of its congeners with the exception of *P. brevis*. The number of horizontal rows of scales between the pelvic-fin insertion and the lateral line demonstrate only a limited degree of overlap between *P. lacustris* and *P. brevis*, with *P. lacustris* having 8 to 11 scales in that series with only 8 of 51 specimens from which that count was taken having 8 scales, whereas *P. brevis* has 6 to 8 scales in that series with only 3 of the 59 specimens from which that count was taken having 8 scales in that series (see also Figure 36). The two species, both endemic to northeastern Brazil, also demonstrate distinctly different, albeit overlapping, ranges in the number of lateral-line scales (Figure 37). Because of the cited differences in these features and the allopatry of the populations, they are considered to be distinct species herein.

Remarks.—Steindachner's (1907:152) description of *Prochilodus lacustris* was based upon specimens collected during an expedition that he lead in 1903 to the state of Piauí, northeastern Brazil. Of the extant type material of this species in the Naturhistorisches Museum Wien (NMW), all collected in Lago de Parnaguá, Rio Gurguéia system, we herein designate NMW 56674:4 (124.6 mm SL), the syntype in the best overall condition, as the lectotype. The remaining four syntypes (NMW 56674:1–3 and 5, 85–123.1 mm SL) consequently become paralectotypes.

Perhaps as a consequence of being endemic to the Rios Mearim-Grajaú and Parnaíba, northeastern Brazil, an area relatively poorly sampled ichthyologically, *Prochilodus lacustris* has been rarely cited in the literature. Steindachner (1915:21) did, however, place *P. lacustris* as a junior synonym of *P. argenteus* following his comparison of samples of *P. argenteus* that originated in the Rio São Francisco with specimens of *P. lacustris* that were collected in the Rio Parnaíba. The basis for Steindachner's synonymy of *P. lacustris* into *P. argenteus* was not explicitly stated, but it may have been a consequence of the pronounced similarity in overall head and body form and in scale counts between the two nominal forms. Contrary to Steindachner (1915), we find *P. lacustris* to be distinct from *P. argenteus*, with the former species endemic to the Rios Mearim-Grajaú and Parnaíba drainages. The two species differ in various features, most trenchantly, in the occurrence of dark, irregular bars on the caudal-fin lobes in *P. lacustris* that are absent in *P. argenteus*.

Presumably Steindachner (1915) erroneously considered the presence of the caudal-fin pigmentation in *P. lacustris* to be a juvenile feature for *P. argenteus*, as indicated by the figures accompanying his account of the latter species (Steindachner, 1915, pl. 1: fig. 4 and pl. 2: fig.1, respectively). Although the illustrated specimen labeled as an adult of *P. argenteus* lacks dark caudal-fin markings (Steindachner, 1915, pl. 2: fig. 1), it is indeed that species, whereas the figured specimen indicated by Steindachner as a juvenile of *P. argenteus* with dark markings of the caudal-fin lobes (Steindachner, 1915, pl. 1: fig. 4) is actually a specimen of *P. lacustris*.

Géry (1977:219) apparently followed Steindachner (1915:21) in considering *P. lacustris* to be a junior synonym of *P. argenteus*. Nomura (1984:54), without comment, erroneously cited *P. nigricans*, a species restricted herein to the Amazon basin as a component of the Rio Parnaíba ichthyofauna. On the basis of the information in that paper and the locality, we consider that citation to be a misidentification of *P. lacustris*.

Material Examined.—59 specimens (53, 57.2–324.3 mm SL).

BRAZIL. *Maranhão:* Rio Medonho, NMW 56618, 2 (2, 134.9–159.3). Caxias, NMW 56621, 1 (103.6). Rio Grajaú, MZUSP 5064, 9 (9, 57.2–111.0), MZUSP 20693, 2 (cleared and counterstained for bone and cartilage). Lago de Viana, Viana, MZUSP 36460, 4 (4, 168.0–250.0). *Piauí:* Lago de Parnaguá, Parnaguá, Rio Gurguéia system, NMW 56623, 1 (59.1); NMW 56674:1, 1 (123.1, paralectotype of *Prochilodus lacustris*) [1R]; NMW 56674:2, 1 (100.1, paralectotype of *Prochilodus lacustris*) [IR]; NMW 56674:3, 1 (85.0, paralectotype of *Prochilodus lacustris*) [1R]; NMW 56674:4, 1 (124.6, lectotype of *Prochilodus lacustris*) [1R]; NMW 56674:5, 1 (118.6, paralectotype of *Prochilodus lacustris*) [1R]. Teresina, MZUSP 36452, 11 (10, 148.6–198.8); NMW 56712:1–3, 3 (2, 189.4–264.2); NMW 56713, 2 (2, 155.1–227.6). Teresina, Rio Parnaíba, MZUSP 4634–37, 4 (4, 63.6–201.0); MZUSP 5104, 6 (6, 58.0–82.2). Barra do Longá (near Buriti do Lopes), Rio Parnaíba, MCZ 46810, 3 (1, 85.0–87.0) [2R]. Lagoa da Missão, NMW 56609:1–3, 3 (3, 205.3–324.3). Campo Maior, Rio Sorubim, tributary of Rio Longá, Fazenda Água Limpa, near highway BR 343, MZUSP 74953, 3 (3, 105.0–108.0).

***Prochilodus lineatus* (Valenciennes, 1836)**

Figures 43, 46; Table 11

Pacu lineatus Valenciennes in D'Orbigny, 1836: no page, pl. 8: fig. 3 [type locality: designated by Valenciennes in Cuvier and Valenciennes (1850:84) as la rivière de la Plata à Buénos-Ayres ((=Argentina) Río de La Plata at Buenos Aires)].—Müller and Troschel, 1844:84 [America meridionali (=southern America)]; 1845:8 [same information as in Müller and Troschel, 1844].—Valenciennes in D'Orbigny, 1847:9 [distinguished from curimatids; brief description].

Paca lineatus Jardine, 1841:258 [Guiana; generic name modified].—Valenciennes in D'Orbigny, 1847, pl. 8: fig. 3 [illustration of species].

Prochilodus lineatus.—Valenciennes in Cuvier and Valenciennes, 1850:84 [la rivière de la Plata à Buénos-Ayres (=Río de la Plata, at Buenos Aires)].—Günther, 1864:295 [based upon Valenciennes, 1850].—Lütken, 1875b:193 [Plata-Flodens (=Río de la Plata)].—Steindachner, 1881:130 [Argentina, Province of Buenos Aires].—Eigenmann and Eigenmann, 1891:48 [in listing of South American fishes].—Boulenger, 1897:3 [Bolivia, Chaco, Mission de San Francisco].—Evermann and Kendall, 1906:79 [similarity to *Prochilodus platensis* noted].—Eigenmann et al., 1907:151 [La Plata basin].—Eigenmann, 1907a:451; 1910:424 [in listing of South American fishes]; 1912:271 [similarity to *P. maripicru*].—Devincenzi, 1925a:99 [Uruguay].—Devincenzi and Barattini, 1926, pl. 11: fig. 2 [Uruguay].—Fowler, 1932:345 [Brazil, Mato Grosso, Descalvados]; 1950:220 [literature compilation]; 1975:359 [literature compilation].—MacDonagh, 1934:49 [Argentina].—Pearson, 1937b: 109 [Río Paraguay basin].—Devincenzi and Legrand, 1940:6, pl. XI [index, Uruguay; illustration].—Devincenzi and Teague, 1942:60 [middle Río Uruguay].—Pozzi, 1945:258 [Argentina].—Buen, 1950:87 [Uruguay].—Saul, 1975:112 [comments on feeding].—Géry, 1977:219 [in part, not citation for Rio São Francisco].—Pauls and Bertollo, 1984:787 [karyotype].—Bertoletti, 1985:100 [Brazil, Rio Uruguai]; 1986:275 [Rio Grande do Sul].—Bertollo et al., 1986:156, table 1 [karyotype].—Ferraz de Lima, 1987:88 [Brazil, Mato Grosso, Rio Cuiabá; major importance in fishery].—Géry et al., 1987:436 [Paraguay, Río Paraguay; Argentina].—Godoy, 1987:179 [Río de La Plata basin].—López et al., 1987:19 [Argentina].—Petrere, 1989:5 [economic importance].—Bertoletti et al., 1990:46 [Brazil, Rio Uruguai].—Carozza and Cordiviola de Yuan, 1991:119 [age and growth studies].—Menin and Mimura, 1992:523 [feeding modifications].—Cordiviola de Yuan and Campana, 1993:327 [scale development].—Rossi, 1993:159 [ontogeny of dentition and digestive system; food items through ontogeny].—Sverlij et al., 1993:1 [biology and fisheries].—Fugi et al., 1996:297 [daily feeding periodicity and food items].—Agostinho et al., 1997:184 [Brazil, upper Rio Paraná; abundance in most localities].—Britski et al., 1997:72, figs. on pages 72, 73 [Brazil, Pantanal].—Pavanelli and Caramaschi, 1997:26, table 1 [Brazil, Paraná, Rio Paraná basin].—Revaldaves et al., 1997:381 [Brazil, upper Rio Paraná; within basin genetic variability].—Mochek and Pavlov, 1998:28 [Bolivia, Río Pilcomayo; ecology].—Agostinho and Julio, 1999:382, table 16.1 [Brazil, Rio Paraná].—Benneman et al., 2000:14, 16 [Brazil, Paraná, Rio Tibagi].—Kas'yanov and Izyumov, 2000:353 [Bolivia, Río Pilcomayo; age and growth].—Fugi et al., 2001:27 [Brazil, Rio Paraná; trophic morphology].—Nakatani et al., 2001:198, figs. 57, 58 [descriptions of eggs, larval, and juvenile stages].—Sivasundar et al., 2001:413 [Río de La Plata basin; high levels of gene flow within basin].

Curimatus lineatus.—Valenciennes in Cuvier and Valenciennes, 1850:90, cited as synonym of *Prochilodus lineatus* (Valenciennes, 1836)].

Prochilodus reticulatus [not of Valenciennes, 1850].—Kner, 1859:147 [Brazil, Irisanga].—Günther, 1864:295 [in part, based upon Kner, 1859, Brazil citation].—Perugia, 1891:640 [Argentina, upper Río Paraná].—Eigenmann, 1910:424 [in part, citation of species in Alta Parana (= upper Rio Paraná)].—Bertoni, 1914:10 [Paraguay]; 1939:54 [Paraguay].—Fowler, 1950:222 [in part, cited occurrence of species in Río Paraguay].—Ringuelet, 1975:62 [citations for Paraná and Paraguay basins; not citation for Amazon basin].—López et al., 1987:19 [Argentina].—[Not Pearson, 1937b:109; Ringuelet and Aramburu, 1961:37.

Prochilodus nigricans [not of Agassiz, 1829].—Weyenberg, 1877:5 [Argentina: Tucuman (Río) Paraná, (Río) Uruguay, (Río) Bermejo, (Río) Salado].—Bertoni, 1914:10 [Paraguay]; 1939:54 [Paraguay].—Eigenmann and Allen, 1942:57 [in part, citation of species in (Río de) La Plata basin].—Pozzi, 1945:258 [Argentina].—Fowler, 1950:221 [literature compilation, in part; not citations of species from Paraguay].—Ringuelet, 1975:72 [upper and lower Río Paraguay].—Nomura, 1984:54 [Brazil, common name].—López et al., 1987:19 [Argentina].

Prochilodus scrofa Steindachner, 1881:129 [page 29 of separate], pl. 6: fig. 2 [type locality: Umgebung von Rio Janeiro vielleicht aus dem Rio Parahyba (= Brazil), vicinity of Rio de Janeiro, perhaps Rio Paraíba do Sul; restricted herein to Brazil, Rio de Janeiro, Rio Paraíba do Sul].—Eigenmann and Eigenmann, 1891:48 [in listing of South American fishes].—Ulrey, 1895: 260 [Brazil].—Eigenmann and Norris, 1900:355 [Brazil, Piracicaba].—Eigenmann and Kennedy, 1903:511 [Paraguay, Asuncion, Estancia Armonia, Arroyo Termentina; Brazil, Piracicaba].—Eigenmann et al., 1907:124 [Paraguay, Bahia Negra].—Eigenmann and Ogle, 1907:5 [cited similarity to *P. beani*].—Eigenmann, 1910:424 [in listing of South American fishes].—Bertoni, 1914:10 [Paraguay]; 1939:54 [Paraguay].—Pearson, 1937b:109 [Río Paraguay].—Campos, 1945:451 [Brazil, São Paulo, Rio Mogi-Guaçu].—Pozzi, 1945:258 [Argentina].—Fowler, 1950:223 [literature compilation]; 1975:360 [literature compilation].—Ringuelet and Aramburu, 1961:37 [Argentina; common name].—Bonetto, 1963:14, fig. 2 [migration].—Ringuelet et al., 1967:204 [Río Paraguay and Río Paraná].—Britski, 1972:83 [Brazil, São Paulo, Rio Paraná].—Roberts, 1973b:214 [nocturnal spawning].—Godoy, 1975:44, 66, 633 [tagging, details of anatomy, economic importance, life history, growth, longevity].—Lowe-McConnell, 1975:110 [spawning grounds]; 1979:233 [partial spawning; number of ova]; 1984:143 [economic importance]; 1987:155 [fish tagging; speed of migration].—Ringuelet, 1975:59 [Río Paraná basin].—Géry, 1977:222 [Rio de Janeiro; Río Paraguay].—Galetti et al., 1984:403 [karyotype].—Nomura, 1984:54 [Brazil, common name].—Pauls and Bertollo, 1984:787 [karyotype].—Bertoletti, 1985:100 [Brazil, Rio Uruguai]; 1986:275 [Brazil, Rio Grande do Sul].—Northcote et al., 1985:2707 [effects of impoundment on populations identified as *P. scrofa*].—Bertollo et al., 1986:156, table 1 [karyotype].—Godoy, 1986:41 [Brazil, Rio Paraná].—Toledo et al., 1986: 447 [speed of migration in upper Rio Paraná, Brazil].—Géry et al., 1987: 436 [Paraguay, Río Paraguay, Río Paraná].—López et al., 1987:19 [Argentina].—Nupelia, 1987:43 [Brazil, Itaipu Reservoir; common name; economic importance].—Toledo et al., 1987:501 [Brazil, Rio Paraná, Rio Mogi-Guaçu].—Petrere, 1989:3 [economic importance; upper Rio Paraná].—Anonymous, 1991:30 [as most commercially important species in Itaipu reservoir; biology].—Fugi and Hahn, 1991:873 [diet and feeding modifications].—Godinho et al., 1991:64 [ability to ascend fish ladders].—Petrere et al., 1991:126 [growth rates].—Santos and Barbieri, 1991:12 [age and growth].—Menezes and Vazzoler, 1992:62 [reproductive characteristics].—Agostinho et al., 1993:180, table 1 [Brazil; Rio Paraná, reproduction below Itaipu Reservoir].—Agostinho et al., 1993:182 [Brazil, Itaipu Reservoir; fisheries].—Sverlij et al., 1993:2 [biology and fisheries].—Agostinho and Julio, 1999:397 [Brazil, Itaipu Reservoir].—Sivasundar et al., 2001:414 [genetic similarity of populations in upper Rio Paraná with those from other portions of Río de La Plata basin].—Marçal-Simabuku and Peret, 2002:299 [Brazil, São Paulo, Rio Mogi-Guaçu; seasonal diet].—[Not Petrere, 1985:1.]

Prochilodus platensis Holmberg, 1888:898 [type locality: Argentina, Buenos Aires, Río de la Plata, Buenos Aires]; 1889:375 [Argentina; common name]; 1891:186 [Argentina, Río de La Plata; redescription].—Lahille, 1895:271 [Argentina].—Evermann and Kendall, 1906:79 [Argentina; similarity to *Prochilodus lineatus* noted].—Eigenmann and Ogle, 1907:5 [cited similarity to *P. beani*].—Eigenmann, 1910:424 [in listing of South American fishes].—Devincenzi, 1925a:103 [Uruguay].—Fowler, 1926:261 [Argentina, Buenos Aires]; 1950:222 [literature compilation]; 1975:359 [literature compilation].—Ringuelet, 1940:99 [Argentina, Rosario]; 1975:44 [Río de La Plata basin].—Pozzi, 1945:258 [Argentina].—Angelescu and Gneri, 1949: 214 [digestive system morphology].—Ringuelet and Aramburu, 1961:37 [Argentina; common name].—Bonetto, 1963:24 [migration].—Ringuelet et al., 1967:204 [Argentina, Río de La Plata basin; biological data; common name].—Mago-Leccia, 1972:47 [use of caudal-fin pigmentation to distinguish species groups].—Oliveros and Occhi, 1972:121 [buccopharyngeal anatomy].—Bayley, 1973:26 [Río Pilcomayo in Bolivia and Argentina; migration; spawning].—Pignalberi and Cordiviola de Yuan, 1973:29 [Argentina, middle Río Paraná; conspecificity of various morphs].—Cordiviola de Yuan, 1974:217 [Argentina, Río Paraná].—Bonetto, 1975:196, table 6 [ecology, biomass]; 1994:447, 454 [dominance in lentic environments of Río Paraná; reduction of populations of species in impoundments].—Godoy, 1975:67 [economic importance]; 1987:180 [Río de La Plata basin].—Lowe-McConnell, 1975:109 [abundance]; 1984:143 [economic importance]; 1987:153 [abundance].—Géry, 1977:222 [as possible synonym of *P. lineatus*].—Bonetto, Neigg et al., 1978:73 [Argentina, Corrientes].—Bonetto, Neigg et al., 1978:81 [Argentina, Corrientes].—Bonetto, Roldan et al., 1978: 1 [Argentina, Corrientes].—Bonetto et al., 1981:79 [Argentina, Corrientes].—Cione and Tonni, 1981:4 [Argentina].—Arratia et al., 1983:80, 90, table 3 [Argentina, Río Bermejo].—Bowen, 1983:60 [adaptations for detritivory].—Bowen et al., 1984:1120 [utilization of detritus].—Miquelarena, 1984: 614 [caudal fin].—Cordiviola de Yuan and Pignalberi de Hassan, 1985:214 [lower Río Paraná, Diamente and San Pedro regions]; 1989:43 [Argentina, Río Paraná; population density].—Petrere, 1985:1 [importance in fisheries].—López et al., 1987:18 [Argentina].—Casciotta et al., 1989: 607 [Argentina, Río Dulce].—Miquelarena et al., 1990:272, table 1 [Argentina, Tucuman, Río Sali basin].—Haro et al., 1991:252 [Argentina, Río Quarto].—Petrere et al., 1991:126 [growth rates].—Bistoni et al., 1992:107 [Argentina, Río Dulce].—Menezes and Vazzoler, 1992:62 [reproductive characteristics].—Menin and Mimura, 1992:523 [feeding modifications].—Menni et al., 1992:136, table 2 [Argentina, Río Pilcomayo-Paraguay basins].

Prochilodus argenteus [not of Agassiz, 1829].—Perugia, 1891:640 [Argentina, central Chaco, Resistencia].—Eigenmann et al., 1907:151 [in part, Río de La Plata basin citations].—Eigenmann, 1910:424 [in listing of South American fishes; in part].—Bertoni, 1939:54 [Paraguay].—Ringuelet, 1975:72 [upper and lower Río Paraguay].—López et al., 1987:18 [Argentina].

Prochilodus costatus [not of Valenciennes, 1850].—Eigenmann, 1910:424 [in listing of South American fishes; citation of occurrence in Río Paraguay basin].

Salmo novemradiatus Larrañaga, 1923:387 [not seen; publication based upon manuscript prepared in 1814; species originally cited as *Salmo 9-radiatus;* information based upon Devincenzi (1925b:312) and Eschmeyer et al., in Eschmeyer, 1998].—Devincenzi, 1925b:312 [*Salmo novemradiatus* equated with *Prochilodus lineatus*].

Prochilodus affinis [not of Lütken, 1875a].—Fowler, 1950:215 [literature compilation in part; not cited occurrence of species outside of Río de la Plata basin].

Prochilodus hartii [not of Steindachner, 1874].—Fowler, 1950:218 [literature compilation, in part; not cited occurrence of species in Brazil, São Paulo].—Ringuelet, 1975:59 [Argentina, Río Paraná basin].

Prochilodus marcgravei.—Ringuelet et al., 1967:204 [in part, Argentinian records].—[Not Ringuelet and Aramburu, 1961:37; Ringuelet, 1975:61.

DIAGNOSIS.—The lack of dark, irregular, wavy, bar-like patterns on the caudal-fin lobes discriminates *Prochilodus lineatus* from *P. brevis, P. lacustris, P. mariae, P. nigricans,* and *P. rubrotaeniatus*, which have such caudal-fin pigmentation. Within the group of species with hyaline caudal fins, *P. lineatus* differs from *P. vimboides* in the number of scales along the lateral line (44 to 50 versus 34 to 39, respectively), the number of horizontal rows of scales around the caudal peduncle (17 to 21 versus 13 to 15, respectively), and the number of vertebrae (42 to 44 versus 36 to 39, respectively); from *P. britskii* in the number of horizontal rows of scales around the caudal peduncle (17 to 21 versus 13 or 14, respectively); the number of vertebrae (42 to 44 versus 39 or 41, respectively), and the number of teeth in the inner row of each side of the lower jaw (9 to 18 teeth versus 6 or 7, respectively); from *P. hartii* in the number of scales in the lateral line (44 to 50 versus 40 to 43, respectively), the number of horizontal rows of scales around the caudal peduncle (17 to 21 versus 14 to 16, respectively), and the number of vertebrae (42 to 44 versus 37 to 40, respectively); from *P. magdalenae* in the number of vertebrae (42 to 44 versus 39 to 42, respectively), the presence of dark, wavy, horizontal stripes on the lateral surface of the body (versus the lack of such pigmentation in *P. magdalenae*), and, less discretely, in the number of scales in the lateral line (44 to 50, 47 and 48 most frequent and 44 to 46 in only 10 of 122 specimens from which this count was taken, versus 43 to 46, 44 and 45 most frequent with 46 in only 3 of 41 specimens examined from which this count was taken, respectively); from *P. argenteus* in the number of horizontal rows of scales between the dorsal-fin origin and the lateral line (7 to 10, 9 most frequent, 8 common, and 10 infrequent, versus 10 or 11, 11 most frequent, respectively; Figure 33), the number of median predorsal scales (14 to 20, 16 most frequent, versus 17 to 22, 18 to 21 about equally frequent and 17 rare, respectively; Figure 34), and the number of scales along the lateral line (44 to 50, 47 most frequent, versus 45 to 51, 48 most frequent, respectively); from *P. reticulatus* in the number of vertebrae (42 to 44 versus 38 to 40, respectively), the presence of distinct wavy, dark, horizontal stripes along the lateral surface of the body (versus the absence of such stripes in *P. reticulatus*), and less distinctly in the number of lateral-line scales (44 to 50, with 47 most frequent, versus 41 to 45, with 43 most frequent, respectively); and from *P. costatus* in the number of scales along the lateral line (44 to 50, 47 most frequent and 44 to 46 less frequent, versus 44 to 47, 45 most frequent and 47 in only 2 of 32 specimens examined for this feature, respectively; Figure 41), and in the number of vertebrae (42 to 44, with 43 in 63.0% of specimens examined for this feature, versus 41 to 43, with 41 and 42 about equally frequent and 43 in only 6.7% of specimens examined for this feature; Figure 42).

DESCRIPTION.—Morphometric and meristic data for *Prochilodus lineatus* presented in Table 11. Body moderately high, transversely compressed. Greatest body depth at dorsal-fin origin. Dorsal profile of head gently concave. Predorsal profile of body convex. Dorsal profile of body posteroventrally inclined along dorsal-fin base, ranging from gently convex to straight from posterior of dorsal-fin base to adipose-fin origin, and concave along caudal peduncle. Predorsal portion of body gently ridged medially. Postdorsal portion of body obtusely rounded transversely. Ventral profile of body moderately convex from tip of lower jaw to posterior of anal-fin base. Ventral profile of caudal peduncle concave. Prepelvic region transversely flattened proximate to pelvic-fin insertion. Poorly developed median keel present between pelvic-fin insertion and anus.

Head profile pointed. Mouth terminal. Snout length greater than horizontal width of orbit. Nares of each side of head close to each other; anterior nares circular, posterior nares crescent shaped. Adipose eyelid present but poorly developed; most developed anteriorly, but with greater part of eye uncovered. Lips fleshy, moderately developed relative to those of some other prochilodontids, and forming oral disk when protracted.

Functional teeth in two rows in each jaw. All teeth movably implanted in flesh that overlies jaws. All teeth of similar size, with exposed portion spoon shaped from frontal view except when worn down. Inner tooth series in each jaw of protracted mouth with 13 to 25 teeth on left side of upper jaw and 9 to 18 teeth on left side of lower jaw. Outer row of teeth in each jaw with approximately 95 teeth on each side of upper jaw and approximately 75 teeth on each side of lower jaw in examined specimens. Upper and lower lips bordered by numerous globular, fleshy papillae.

Scales spinoid. Scales in middorsal series between posterior of dorsal-fin base and adipose-fin origin similar in form to those of adjoining regions of body. Lateral line with 44 to 50

TABLE 11.—Morphometrics and meristics of *Prochilodus lineatus:* (A) lectotype of *Prochilodus scrofa,* NMW 56702; and (B) all specimens of *Prochilodus lineatus* from which counts and measurements were taken. Standard length is presented in mm; values 2 to 16 are percentages of SL, 17 to 21 are percentages of HL.

Characters	A	B
	Morphometrics	
1. Standard length	251.1	23.8–460.2
2. Greatest body depth	32.8	30.5–45.7
3. Predorsal length	46.0	40.8–52.6
4. Dorsal-fin base length	16.2	12.1–19.9
5. Dorsal fin to adipose fin distance	28.8	20.7–30.6
6. Dorsal fin to caudal fin distance	44.9	36.3–51.2
7. Prepelvic length	49.7	45.9–62.0
8. Preanal distance	76.1	74.2–82.9
9. Snout to anal-fin insertion	78.7	77.7–86.2
10. Anal-fin base length	10.8	7.2–12.4
11. Caudal-peduncle length	13.5	10.6–15.5
12. Dorsal-fin length	26.1	21.4–38.1
13. Pectoral-fin length	22.3	17.2–23.6
14. Pelvic-fin length	19.5	14.2–25.5
15. Least caudal-peduncle height	12.3	10.7–14.6
16. Head length	26.1	23.0–36.8
17. Snout length	43.7	32.6–48.4
18. Bony orbital diameter	17.7	15.0–30.2
19. Postorbital length	41.2	32.8–51.3
20. Interorbital width	48.9	47.0–59.2
21. Mouth width	43.5	38.5–50.7
	Meristics	
Lateral-line scales	47	44–50
Scale rows between dorsal-fin origin and lateral line	9	7–10
Scale rows between anal-fin origin and lateral line	7	6–9
Scale rows between pelvic-fin insertion and lateral line	8	6–9
Rows of scales around caudal peduncle	17	17–21
Median predorsal scales	16	14–20
Median scales between dorsal and adipose fins	19	13–19
Vertebrae	43	42–44
Inner row teeth, upper jaw	21	13–25
Inner row teeth, lower jaw	13	9–18

(51.2% of specimens with 47) pored scales; 7 to 10 (76.9% of specimens with 9) horizontal rows of scales between dorsal-fin origin and lateral line; 6 to 9 (61.2% of specimens with 8) horizontal rows of scales between pelvic-fin insertion and lateral line; 6 to 9 (58.7% of specimens with 7) horizontal rows of scales between anal-fin origin and lateral line; 14 to 20 (34.5% of specimens with 16) median predorsal scales; 13 to 19 (41.6% of specimens with 15) scales in middorsal series between posterior of dorsal-fin base and adipose-fin origin; 17 to 21 (87.6% of specimens with 18) horizontal rows of scales around caudal peduncle.

Dorsal fin preceded by small, but well-developed, anteroventrally bifurcate, procumbent spine somewhat triangular in lateral view. Dorsal-fin rays (including procumbent spine) iii,9 or 10 (iii,10 most frequent); anal-fin rays iii,7 to 9, or ii,8 (ii,8 most frequent); pectoral-fin rays i,13 to 18 (i,15 most frequent); pelvic-fin rays i,7 or 8 (i,8 most frequent); principal caudal-fin rays 10/9.

Vertebrae 42 to 44 (63.0% of specimens with 43).

Dorsal fin truncate, slightly pointed distally; posterior unbranched and anterior branched rays longest and subequal. Dorsal-fin origin located closer to tip of snout than to caudal-fin base. Greatest length of adipose fin approximately 1.5 times horizontal width of orbit. Adipose-fin origin located along vertical that passes through middle of anal-fin base. Pectoral fin distally pointed. Tip of adpressed pectoral fin reaching posteriorly approximately two-thirds of distance between pectoral- and pelvic-fin insertions. Pelvic fin falcate. Pelvic-fin insertion located along vertical that passes through posterior one-third of dorsal-fin base. Tip of adpressed pelvic fin extending posteriorly approximately two-thirds of distance between pelvic-fin insertion and anus. Axillary scale present, its length approximately one-third of greatest length of pelvic fin. Unbranched posterior and branched anterior anal-fin rays longest and subequal. Caudal fin bifurcate.

COLORATION IN ALCOHOL.—Ground coloration silvery yellow or brownish yellow, with dorsal portions of body and head darker. Lateral surface of body with 8 to 17 dark, irregular, vertically elongate pigment patches between head and caudal fin. Pigment with approximate overall form of narrow isosceles triangles, with apexes positioned along center of ventrolateral portion of body and bases along dorsomedial region of body. Patches well developed in small specimens, but indistinct or absent in large individuals. Lateral surface of body with approximately 8 to 14 dark, wavy, horizontal stripes along dorsal and ventral margins of exposed portions of scales. Approximately 4 to 7 (most frequently 5) wavy stripes above lateral line, and 4 to 7 (most frequently 6) wavy lines below. Field of black or brown chromatophores forming dark, irregularly shaped spot on upper portion of opercle.

Dorsal fin with 2 to 8 (most frequently 5) dark, irregular stripes beginning on anterior margin of fin and extending across fin approximately parallel to fin base. Adipose fin with small dark spots scattered over surface, and margin finely bordered with black. Pectoral, pelvic, anal, and caudal fins dusky. Iris yellowish silver or brownish orange, with diffuse dusky areas on dorsal and ventral portions.

COLORATION IN LIFE.—(Based upon color transparencies of recently collected adults from the upper Rio Paraná basin taken by first author and figure of species in Nakatani et al. (2001)). Dark pigmentation as described above. Ground coloration silvery, with some red pigmentation on lateral surface of body. Dorsal region of body and especially head darker. Dorsal fin hyaline. Pectoral and caudal fins moderately dusky, with pectoral fin sometimes reddish. Pelvic fin red overall, with coloration shifting from bright yellow basally to red distally. Anal fin with interradial membranes dusky and with anterior and posterior margins of fin reddish yellow. Iris yellowish silver.

Underwater observations of *Prochilodus lineatus* in different habitats of the Rio Miranda basin, Mato Grosso do Sul, Brazil,

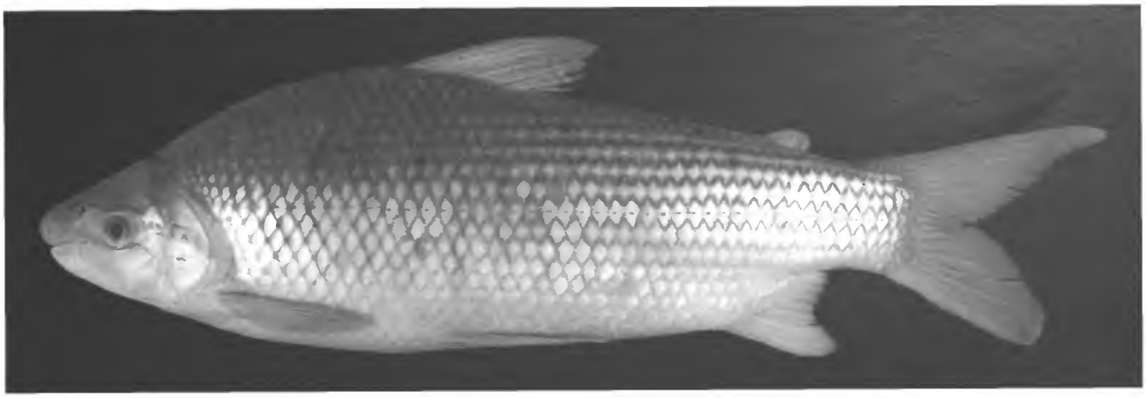


FIGURE 46.—*Prochilodus lineatus*, MZUSP 20864, 325.4 mm SL; Brazil, São Paulo, Usina do Limoeiro, Rio Pardo.

by the authors showed that, although populations in large channels demonstrated the life coloration just described, populations in tributary, hard-water streams were much darker.

DISTRIBUTION.——*Prochilodus lineatus* is broadly distributed throughout the Rio Paraná-Río Paraguay basin in Argentina, Bolivia, Brazil, Paraguay, and Uruguay (Figure 43, diamonds). We also have examined material of the species that originated in the independent Rio Paraíba do Sul system of the states of São Paulo and Rio de Janeiro, Brazil, and the rivers draining into northern portions of Lagoa dos Patos in the state of Rio Grande do Sul, Brazil. In addition to the localities from which specimens examined in this study originated, the species also occurs in the southern portions of the Lagoa dos Patos, Brazil (Roberto E. Reis, MCP, pers. comm., 2002), the Río Sali and Río Dule systems that drain into the Mar Chiquita basin of the state of Córdoba, Argentina (Sverlij et al., 1993:5, fig. 2), and south of the mouth of the Río de La Plata in the Río Salado and Laguna de Chascomús of Argentina (Sverlij et al., 1993:5, fig. 2).

ECOPHENOTYPIC VARIATION.—The broad range in the overall form of the body in *Prochilodus lineatus* from different habitats was discussed by Sverlij et al. (1993:3). Those authors noted that previous research by Cabrera and Candida (1964), Vidal (1967), and Pignalberi and Cordiviola de Yuan (1973) revealed distinctly different body forms among various populations of the species, with the variation apparently correlated with biotic and abiotic features of the habitat. Underwater observations of the species in the region of Bonito, Mato Grosso do Sul, Brazil, by the authors confirmed these earlier observations. Specimens of *P. lineatus* seen feeding on the nutrient poor sandy substrates of tributary streams had thicker lips and more attenuate bodies with an almost straight ventral profile of the body than did individuals of the species in the main river, a habitat with more hard substrate surfaces covered by periphyton.

COMMON NAME.—Corimbatá, curimbatá, curimba, grumatã (Brazil), and sábalo (Argentina, Paraguay, Uruguay, and Bolivia).

BIOLOGY AND FISHERIES.—*Prochilodus lineatus* is one of the commercially most important fish species throughout the Río de La Plata basin. Life history and fisheries information for the species throughout the Argentinian portions of its distributional range was summarized by Sverlij et al. (1993).

COMPARISONS.—As indicated in the "Diagnosis," *Prochilodus lineatus* is unequivocally different in one or more meristic or pigmentary features from all congeners except for *P. argenteus* and *P. costatus*. *Prochilodus lineatus* of the Río de La Plata basin and the Rio Paraíba do Sul basin and *P. argenteus* that is endemic to the Rio São Francisco system, although having an overlap in the number of median predorsal scales and the number of horizontal rows of scales between the lateral line and the dorsal-fin origin, nonetheless, demonstrate pronounced differences in the modal counts for those values (see Figure 34 for median predorsal scales). In light of those differences and the allopatry of the nominal forms, we recognize them as distinct species in this study.

Prochilodus lineatus, in turn, although overlapping *P. costatus* of the Rio São Francisco basin in lateral-line scale counts, has a distinctly different range of modal values for this feature (Figure 41) and has shifted ranges and modally different values for the number of vertebrae (Figure 42). Because of these differences and the allopatry between these two nominal forms, we recognize them as distinct species.

REMARKS.—Valenciennes' (1836, pl. 8: fig. 3) description of *Pacu* (= *Prochilodus*) *lineatus* was based, in part, upon material collected by D'Orbigny in the Río de La Plata, at Buenos Aires, Argentina. No type material for the species was reported in the holdings of the Museum National d'Histoire Naturelle (MNHN) by Bertin (1947) or Eschmeyer et al. (in Eschmeyer, 1998:913). We similarly were unsuccessful in locating the types of this species, and it is likely that none are extant. Nonetheless, the original description and accompanying illustrations (Valenciennes, 1836, pl. 8: fig. 3) make it clear that the species described by Valenciennes is the form treated herein as *Prochilodus lineatus*. Furthermore, the only other *Prochilodus* species known to occur in the broader Rio Paraná-Paraguay basin is *P. vimboides*, a species whose distribution is limited to the northeastern portion of the Río de La Plata basin and rivers of eastern Brazil, areas that are distant from the type locality of *P. lineatus* in the lower Río de La Plata basin. In addition to the differing geographic distributions of the two species, *Prochilodus vimboides* has larger and, thus, fewer scales than does *P. lineatus* and lacks the multiple dark, wavy, longitudinal stripes along the lateral surface of the body that characterize *P. lineatus*.

The broad geographic distribution and consequent intraspecific variability demonstrated by *Prochilodus lineatus* has engendered a number of nomenclatural problems. Many of these problems were an outgrowth of the difficulty earlier authors confronted during their attempts to evaluate the significance of such variation in the absence of adequate population samples from across the range of the species. These factors, in combination, resulted in the formal description of several nominal species for what are now recognized to be geographic variants of *P. lineatus*. Morphologically based comparisons in this study have failed to reveal any basis for the recognition of more than one species within what is herein considered to be *P. lineatus*. Analysis of the mitochondrial DNA sequences from samples of *P. lineatus* that originated at a number of localities across the Río de La Plata basin similarly failed to demonstrate any geographical pattern to the variation in these sequences within that species. That result suggests high levels of gene flow among *P. lineatus* populations within the basin that is presumably associated with the large-scale migrations typical of the species (Sivasundar et al., 2001).

Holmberg (1888:898) described *Prochilodus platensis*, also from the Río de La Plata at Buenos Aires, Argentina, on the basis of a market specimen of approximately 455.0 mm SL. None of the type series of the species described by Holmberg are known to be extant (M. Azpelicueta, in litt., 1987); however, Nani (in Angelescu and Gneri, 1949:214) proposed that *P. platensis* was synonymous with the previously described *P. lineatus*. Despite the lack of type specimens for either nominal species, the information in the original description of *P. platensis* (Holmberg, 1888:898) in conjunction with the subsequent redescription of that species by Holmberg (1891:186–187) make it clear that *P. platensis* falls within the range of variation of *P. lineatus* thereby making it a junior synonym of *P. lineatus*. We consequently consider all of the numerous literature citations of *P. platensis* from the Río de La Plata basin to refer to *P. lineatus*.

Ringuelet et al. (1967:204) similarly considered *P. lineatus* and *P. platensis* to be conspecific, given that they list "*Paca* [sic] *lineatus* Valenciennes en D'Orbigny" as the first entry in the synonymy of the species that they identified as *Prochilodus platensis*. This entry by Ringuelet et al. (1967) is, in turn, followed by several citations of *Prochilodus lineatus* that predate the Holmberg (1889) description of *P. platensis*. Ringuelet et al. (1967) provided no justification for their decision to utilize *P. platensis*, a name that is the junior available synonym by several decades, rather than *P. lineatus*, the oldest available name for this species, nor do we know of any justification for such a practice.

Prochilodus scrofa is the name applied by numerous authors to the populations of what is herein considered to be *P. lineatus* that inhabits the Rio Paraná upriver of the Sete Quedas rapids and in the Rio Paraiba, an independent system draining portions of the states of São Paulo, Rio de Janeiro, and Minas Gerais that empties into the Atlantic Ocean (see synonymy at beginning of species account). Although the Sete Quedas falls has served as a barrier for most groups of fishes (e.g., the Curimatidae, Vari, 1988:358) prior to their inundation by the Itaipu Reservoir in 1983 (Reis et al., 1992:271), no differences were found to justify the recognition of populations of *P. lineatus* above and below the now inundated Sete Quedas rapids as distinct species. As shown in Table 11, *P. scrofa* does not differ morphologically from, and is consequently placed as a junior synonym of, *P. lineatus*. In their analysis of Mitochondrial DNA sequences, Sivasundar et al. (2001:413) found no significant association between genealogy and geographic location of examined *P. lineatus* specimens from across the Río de La Plata basin. In particular, they found that samples of the species from the upper Río Paraná had control region haplotypes that were closely related to those found 2600 river km away in the western tributaries of the lower portion of the Río de La Plata basin. Such genetic continuity across these vast distances is supportive of the hypothesis of the conspecificity of populations, herein considered to be *P. lineatus*, from throughout the Río de La Plata basin and supports the synonymy of *P. scrofa* into that species.

Steindachner's description (1881:129–130, pl. 6: fig. 2) of *Prochilodus scrofa* was based upon two specimens that, according to that author, originated at Rio de Janeiro, Brazil, "perhaps from the Rio Paraíba" (= Rio Paraíba do Sul; translation ours). No prochilodontids are known to inhabit the rivers that flow through the city of Rio de Janeiro. The cited type locality may consequently refer either to the shipping point of the specimens of *P. scrofa* or more likely to the state of Rio de Janeiro that is partially drained by the Rio Paraíba do Sul basin in which *P. scrofa* occurs.

Only one of the two syntypes of *P. scrofa* mentioned by Steindachner in the original description of the species was located in the holdings of the Naturhistorisches Museum, Wien (NMW). This syntype (NMW 56702, 251.1 mm SL), the only one available for examination, is herein designated as the lectotype of the species. If subsequently located, the second specimen mentioned in the original description of the species would become a paralectotype.

Larrañaga (1923) proposed a series of fish names in a manuscript on the botany and zoology of Uruguay that was prepared in 1814 but remained unpublished for almost 11 decades. The lengthy hiatus between the preparation and formal publication of the manuscript resulted in the generic concepts of fishes in the eventual paper being distinctly outdated when published. One of the fish species described by Larrañaga (1923:387), *Salmo novemradiatus* (originally cited as *Salmo 9-radiatus*), was equated by Devincenzi (1925b:312) with *Prochilodus lineatus*. That synonymization seems appropriate because it was based both upon the information in the brief original description of *Salmo novemradiatus* by Larrañaga (1923) and upon the given common name of "Sabolo" reported by Larrañaga for his nominal species, a vernacular name that is still utilized for *Prochilodus lineatus* in the region from which the holotype of *Salmo novemradiatus* originated (Devincenzi, 1925b:312; Ringuelet et al., 1967:204).

The occurrence of populations of *Prochilodus lineatus* in the coastal Rio Paraíba do Sul of the states of São Paulo and Rio de Janeiro in addition to the broad distribution of the species across the Río de La Plata basin at first raises the question of whether the occurrence of the species in the Rio Paraíba do Sul basin is natural or rather the consequence of an introduction by humans. Comparisons within the Prochilodontidae reveal, however, that the only other member of the family that occurs in the Rio Paraná-Paraguay basin, *P. vimboides,* also has a distribution in both the Rio Paraíba do Sul and the upper Rio Paraná that partially matches that of *P. lineatus* (compare Figures 43, 52), which may indicate previous continuity between at least components of those river systems. Geological evidence also indicates that there was a past continuity between what are now the upper portions of the Rio Paraíba do Sul and the upper portions of the upper Rio Paraná, specifically the upper Rio Tietê (see Malabarba, 1998:81, and papers cited therein). In light of the geological evidence and the similarity in the distributions of the two *Prochilodus* species (*P. lineatus, P. vimboides*), we consider it likely that the present distribution of *P. lineatus* in the Rio Paraíba do Sul drainage system to be natural rather than the consequence of human actions.

All of the citations of *P. nigricans, P. hartii, P. reticulatus, P. costatus,* and *P. argenteus* (and their synonyms) for the Rio Paraíba do Sul basin and Paraná-Paraguai system are erroneous, given the absence of these forms in those river systems. These citations are, however, equivocal as they may refer to either *P. lineatus* or *P. vimboides,* or an admixture of the two species. Because of that uncertainty, such references cannot be included with certainty in the synonymy for either of those species.

MATERIAL EXAMINED.—785 specimens (186, 23.8–460.2 mm SL; partial meristic data taken from 120 additional specimens).

ARGENTINA. *Buenos Aires:* Buenos Aires, BMNH 1880.4.1:4–5, 2 (1, 453.2–460.2); CAS 11631 (formerly IU 11354), 2 (1, 190.0–233.4) [1R]; CAS 19251, 1 (317.2) [1R]; CAS-SU 31561, 1 (192.8) [1R]; CAS-SU 40107, 14 (1, 47.1–77.4); MNHN A.9905, 1 (62.8); NRM 9720, 1; USNM 176080, 1. Buenos Aires, Río de La Plata, MZUSP 20882, 1 (131.0). La Plata, BMNH 1878.5.16:61–7, 7 (1, 108.2–137.5) [2R]; BMNH 1908.8.29:16, 1 (333.1); BMNH 1912.6.18:1, 1 (316.3). *Formosa:* Formosa, BMNH 1971.2.12:17, 1 (94.9) [1R]. *Santiago Del Estero:* Río Dulce, in Santiago del Estero, CAS-SU 31562, 1 (157.8) [1R]; CAS-SU 36000, 2 (1, 172.7–183.7) [2R]. Río Dulce, Termas de Río Hondo, USNM 361245, 9. *Inexact Locality:* Río Uruguay, AMNH 12277, 1 (333.0). ARGENTINA, NRM 7069, 2; NRM 7070, 1; USNM 53432, 1 (246.2).

BOLIVIA. *Santa Cruz:* Río Parapetí, at highway bridge in San Antonio del Parapetí, approximately 40 air km E of Camiri, USNM 304449, 4 (3, 124.8–203.2) [4R]. *Tarija:* Río Pilcomayo, in Villa Montes, USNM 317566, 3 (1, 283.0–306.5).

BRAZIL. *Mato Grosso:* Baía Corandá Grande, Rio Cuiabá, Município de Barão de Melgaço, MZUSP 21547, 2 (1, 228.2–235.0). Rio Sangradouro Grande, Rio Cuiabá, Município de Barão de Melgaço, MZUSP 21596, 6 (2, 256.4–295.0); MZUSP 21601, 1 (102.3). Rio Cuiabá, município de Barão de Melgaço, MZUSP 21667, 1 (250.7). Cáceres, Rio Paraguai, MZUSP 2051, 2 (130.5–170.0). Rio Jauru, fazenda, Pontes e Lacerda, município de Cáceres, MZUSP 21598, 1 (224.4). Município de Cuiabá, Chácara Santa Rita, lagoons along margin of Rio Cuiabá, LIRP 727, 1. Rio Cuiabá, Santo Antônio do Leveger, MZUSP 4414, 2 (116.5–215.6). Ranchão da Lagoa, Município de Santo Antônio do Leveger, MZUSP 21577, 1 (240.0). Reserva de Taiamã, Rio Paraguai, MZUSP 14854, 1 (423.3). Rio Jauru, Porto Esperidião, MZUSP 28101, 1 (272.3). Rio Paraguai, MZUSP 35824, 7 (111.5–149.1). *Mato Grosso do Sul:* Rio Paraná, in front of Jupiá, MZUSP 4029, 7 (1, 148.9–210.2); MZUSP 20716, 8 (193.0–250.0). Baía Bela or Albuquerque, Rio Paraguai, município de Corumbá, MZUSP 21536, 1 (265.0). Corixão, Capão Grande, Nhecolândia, Corumbá, MZUSP 36445, 3 (1, 135.5–166.2). Córrego do Bebedouro, município de Três Lagoas, MZUSP 20825, 1 (124.0). Rio Paraná, Ilha Solteira (drying pool on right bank), MZUSP 21430, 5 (3, 93.8–110.3). Island facing Porto Chinelo, Rio Piquirí, fazenda Santo Antonio do Paraíso, município de Itiquira, MZUSP 36726, 1 (252.5). *Minas Gerais:* Itutinga reservoir, Rio Grande, MZUSP 21508, 2 (1, 290.0–337.0). Rio Paranaíba, projeto Usina Hidrelétrica Bocaina, MZUSP 38880, 9 (3, 96.6–332.2). Rio Sapucaí, MZUSP 1375, 2 (101.9–133.2). *Paraná:* Rio Paraná, Porto Mendes, MZUSP 14697, 1 (402.0); MZUSP 14698, 1 (426.5). Rio Paraná, below Guaíra, MZUSP 20660, 1 (368.9). Rio Paraná, Guaíra (upriver of Sete Quedas rapids), MZUSP 21619, 30 (2, 91.4–178.0). Rio Paraná (below Sete Quedas rapids), MZUSP 21090, 24 (3, 90.7–371.9). Rio Ocoí, close to cachoeira, MZUSP 21794, 1 (174.9). *Rio de Janeiro:* "Rio de Janeiro," probably Rio Paraíba do Sul, NMW 56702, 1 (251.1, lectotype of *Prochilodus scrofa;* see discussion under "Remarks") [1R]. Rio Paraíba (do Sul), São Fidélis, MZUSP 20858, 3 (3, 230.0–245.0). *Rio Grande do*

Sul: Vila Scharlau, São Leopoldo, MZUSP 21185, 1 (100.4). Rio dos Sinos, São Leopoldo, MZUSP 20906, 3 (1, 125.0–126.0). Rio Guaíba, Ponta Grossa, Porto Alegre, MZUSP 20844, 1 (212.4). Rio Uruguai, near São Borja, MZUSP 21373, 1 (367.0). Itaqui, MZUSP 1538, 2 (1, 221.0–221.6). Pools in Rio Vacacaí, Santa Maria, MCP 09405, 5 (2, 73.8–101.3). Rio Grande do Sul, BMNH 1884.2.5:42–3, 1 (389.7). *São Paulo:* Cachoeira de Emas, Rio Mogi-Guaçu, MZUSP 3432, 1 (346.5); MZUSP 3433, 1 (325.7); MZUSP 20695, 1 (198.8); MZUSP 20699, 2 (81.0–86.0); MZUSP 20708, 1 (190.5); MZUSP 20733, 2 (101.7–121.1); MZUSP 20740, 1 (98.0); MZUSP 21457, 16 (3, 113.1–178.4). Município de Santa Rosa do Viterbo, Rio Pardo, Rio Paraná basin, LIRP 227, 58. Rio Pardo, LIRP 671, 1. Pirassununga, Rio Mogi-Guaçu, MZUSP 2935, 1 (224.4); MZUSP 42662 (formerly MZUSP 2058, in part), 1 (257.3). Pirassununga, CAS 11839, 1 (177.0); MZUSP 2070, 2 (121.2–189.3). Lagoa do Scatolin, Pirassununga, MZUSP 21436, 76 (6, 23.8–76.3). Cachoeira de Emas, Pirassununga, MZUSP 20693, 7 (3, 89.2–101.5). Rio Mogi-Guaçu, BMNH 1946.12.23:132-135, 4 (93.3–267.8). Rio Piracicaba, BMNH 1907.7.6:8, 1 (239.5); MZUSP 2005, 1 (153.2); MZUSP 3300, 1 (275.0). Piracicaba, CAS 58887, 1 (111.8); MZUSP 1525, 4 (1, 159.8–192.6); MZUSP 204, 6 (175.0–275.0); MZUSP 2071, 1 (195.0). Piracicaba, Rio Piracicaba, MZUSP 2020, 1 (180.2); MZUSP 2057, 1 (310.0). Rio Pardo, near Santa Rosa de Viterbo, Barragem de Itaipava (21°25′S, 47°20′W), USNM 302519, 2. Rio Pardo, Usina do Limoeiro, MZUSP 4629–4633, 5 (3, 220.0–270.0); MZUSP 20793, 1 (245.0); MZUSP 20864, 5 (1, 247.0–325.4). Rio Aguapeí (Rio Feio), CAS 11799, 1 (136.2); MZUSP 1444, 2 (1, 118.0–123.5). Ilha Solteira, Rio Paraná (drying pool), MZUSP 20871, 7 (165.1–355.0); MZUSP 21435, 10 (2, 109.2–340.7). Município de Luís Antônio, Lagoa do Diogo, Reserva de Jataí, Rio Paraná basin, LIRP 380, 143. Santa Branca, Rio Paraíba do Sul, MZUSP 9718, 1 (319.0); MZUSP 21369, 4 (4, 250.0–305.0). Ribeirão Mato Grosso, Monte Aprazível, MZUSP 3621, 2 (109.1–121.8). Monte Alegre, MZUSP 3684, 1 (243.0). Ribeirão Ponte Nova, MZUSP 3042, 3 (215.0–222.0). Porto Cabral, Presidente Epitácio, Rio Paraná, MZUSP 3810, 1 (275.0). Salto de Itapura, Rio Tietê, MZUSP 20900, 3 (2, 181.1–226.5). Rio Tietê, Penápolis, MZUSP 21380, 1 (230.3). Córrego do Moinho, município de Alfredo Castilho, lagoon to side of river, MZUSP 20832, 5 (2, 126.4–135.5). Rio Paraná, Porto Cabral, MZUSP 20667, 1 (249.3). Rio Grande, Franca, MZUSP 2063, 1 (249.0). Olímpia, MZUSP 1297, 1 (226.9). *Inexact Locality:* Rio Paraná, MZUSP 21384, 1 (73.6).

PARAGUAY. *Alto Paraguay:* Puerto Bahía Negra, Río Paraguay, CAS 11634 (formerly IU 10268), 1 (230.3) [1R]. Río Paraguay between Bahia Negra and Estancia Doña Julia (20°10′S, 58°9′41″W), NRM 22374, 2. *Amambay:* Río Paraguay basin, Río Apa, 1500 m below Bella Vista, NRM 29341, 9; NRM 29342, 9; NRM 29343, 5. *Canendiyu:* Riacho tributary to Río Paraná, in Salto del Guaíra, UMMZ 206413, 6 (1, 86.7–101.8) [1R]. *Central:* Río Paraguay, USNM 181416, 1. Río Paraguay, near Asunción, USNM 181716, 1. W of Asunción, BMNH 1935.6.4:340-344, 8 (1, 35.7–134.0) [1R]. Asunción, Río Paraguay, CAS 59317 (formerly IU 9940–9941), 2 (1, 221.7–224.0) [1R]. Asunción Bay, near Asunción, Río Paraguay, USNM 181717, 4 (1, 133.4–181.0); USNM 181775, 3 (1, 158.2–258.3) [2R]. Río Paraguay, 1 km S of bridge in Puente Remanso, UMMZ 205578, 4 (1, 69.2–99.20) [2R]; UMMZ 205861, 8 (1, 62.9–77.9) [1R]; UMMZ 208092, 4 (1, 119.7–211.6). *Concepción:* Arroyo Trementina, FMNH 52559 (formerly CM 9944-9945), 2 (1, 237.1–241.4) [1R]. Río Ypané, approximately ESE of Concepción, UMMZ 207982, 3 (1, 191.0–248.6) [1R]. Río Paraguay basin, Estancia Laguna Negra, Laguna Negra (27°03′S, 57°01′W), NRM 23122, 5. *Itapuã:* Arroyo Poromoco, 34.5 km N of Encarnación, UMMZ 206112, 5 (1, 67.1–75.7) [5R]. Arroyo San Rafael, 2.2 km NE of San Rafael, UMMZ 206170, 2 (1, 74.8–88.3) [1R]. *La Cordillera:* E shore of Lago Ypacaraí, in San Bernardino, UMMZ 207644, 2 (1, 188.5–198.1) [1R]. *Ñeembucú:* Río Paraguay basin, Arroyo Honda, at crossing of road from Pilar to Humaitá, NRM 32917, 10. Río Paraguay basin, Arroyo Monduosa, at crossing of road at km 7 on road from Pilar to San Juan de Ñeembucú (26°47′55″S, 58°17′07″W), NRM 32910, 1; NRM 32912, 1. Arroyo Funco Cue, small river crossing on road from Pilar to Humaitá, near Humaitá (27°03′51″S, 58°29′35″W), NRM 32887, 5. Paso Cornelio, swamp along road from Pilar to Humaitá (27°03′09″S, 58°25′40″W), near Humaitá, NRM 32833, 4. *Presidente Hayes:* Villa Hayes, FMNH 71225, 3 (1, 31.3–44.9). Flooded area and lagoa approximately 34.3 km NW of bridge in Puente Remanso, UMMZ 207012, 1 (386.4). Río Paraguay, approximately 1.0 km S of bridge in Puente Remanso, UMMZ 208092, 1 (325.9) [1R]. Río Pilcomayo, at bridge approximately 12 km WSW of Chaco-i, UMMZ 207554, 2 (1, 170.7–180.5) [1R]. Río Pilcomayo, at Puente Juan de Perón (24°44′33″S, 58°50′21″W), NRM 25912, 6; NRM 29945, 1. Río Pilcomayo drainage, laguna within military post at General Bruguez (24°44′33″S, 58°50′10″W), NRM 29511, 1. *Inexact Locality:* USNM 1632, 1; USNM 21445, 1.

URUGUAY. *Canelones:* Montevideo, USNM 118018, 1 (340.2): USNM 124491, 2 (1, 326.7–335.9). *Colonia:* Arroyo Rosario drainage, Arroyo Tolla, 500 m upstream from mouth into Arroyo Rosario (34°19′17″S, 57°20′13″W), NRM 36699, 1; NRM 41488, 11; NRM 41489, 11; NRM 41490, 12; NRM 41491, 12; NRM 41492, 10. *Salto:* Salto, Río Uruguay, BMNH 1927.2.9:10, 1 (165.0) [1R]. *Soriano:* Río Uruguay, S of Dolores, FMNH 71229, 4 (1, 112.5–144.0) [1R]. *Inexact Locality:* Uruguay, NMW 56704, 2 (2, 285.4–298.4). Río Uruguay, MCZ 843, 2 (1, 231.5–238.3) [1R].

Prochilodus magdalenae **Steindachner, 1879**

FIGURES 43, 47; TABLE 12

Prochilodus asper var. *magdalenae* Steindachner, 1879a:78 (page 62 of separate), pl. 12: fig. 1 and 1a [name used in caption for two figures but species is cited on page 35 of text as *Prochilodus asper;* type locality: Magdalenen-Strome (= Río Magdalena, Colombia)].

Prochilodus asper [not of Lütken, 1875].—Steindachner, 1879a:51 (page 35 of separate) [Río Magdalena; apparently erroneously cited as *Prochilodus asper* in species account, although associated figure in publication (pl. 12: fig. 1 and 1a) is identified as *Prochilodus asper* var. *magdalenae*]; 1880:67 [Colombia, Río Cauca]; 1902:141 [Colombia, Santander, Río Lebrija].—Posada Arango, 1909:300 [Río Magdalena, Río Cauca].—Fowler, 1975:358 [literature compilation].

Prochilodus rubrotaeniatus [not of Jardine, 1841].—Steindachner, 1880:68 [Colombia, Río Cauca].—Eigenmann and Eigenmann, 1891:48 [in listing of South American fishes; in part, citation of species from (Río) Cauca].—Posada Arango, 1909:300 [Río Cauca].—Miles, 1947:136 [comments on Steindachner, 1880].

Prochilodus magdalenae.—Eigenmann and Eigenmann, 1891:48 [in listing of South American fishes].—Eigenmann and Ogle, 1907:5 [cited similarity to *P. beani*].—Eigenmann, 1907b:768 [lateral-line scale count]; 1910:424 [in listing of South American fishes]; 1920a:6, 11 [Colombia, Río Atrato; *Prochilodus magdalenae* cited as senior synonym of *P. beani* Eigenmann and Ogle, 1907]; 1920b:16 [(Río) Atrato and (Río) Magdalena basins]; 1922a:114 [(Río) Atrato and (Río) Magdalena basins].—Ridoutt, 1939:70 [in key to species of *Prochilodus*].—Fowler, 1942:133 [Colombia, Ríos Atrato, Sucio, Truandó, and Cauca].—Miles, 1943:43, unnumbered fig. on page 46 [Colombia, Río Cauca basin; illustration of external head osteology]; 1947:136, fig. 77 [Río Magdalena basin, upper Río Cauca, Río Atrato]; 1973:38 [Colombia, Río Cauca basin].—Mago-Leccia, 1972:47 [use of caudal-fin pigmentation to distinguish species groups].—Géry, 1977:219 [Colombia].—Cala, 1987:76 [Colombia].—Menezes and Vazzoler, 1992:62 [reproductive characteristics].—Román-Valencia and Acero, 1992:122 [Colombia, Antióquia: coastal rivers, Río León, Río Sucio].—Román-Valencia, 1993a:59 [Colombia, Río Atrato; diet, reproductive biology].—Cala, 1995:49 [Colombia: Río Magdalena basin, Betania Reservoir; reductions of populations in and upriver of impoundment].—Mojica-C., 1999:554 [Colombia, Río Magdalena, Río Cesar, Río San Jorge, Río Cauca, Río Ranchería, Río Sinú].—Sánchez, M. et al., 2000:218 [Colombia, Departamento del Huila, upper Río Magdalena; economic importance].—Instituto Alexander von Humboldt, 2000:184 [Colombia, Río Magdalena basin; endangered].

Prochilodus beani Eigenmann in Eigenmann and Ogle, 1907:5, fig. 2 [type locality: Truando (=Colombia, Chocó, Truandó)].—Eigenmann 1920a:6 [cited as equivalent to *Prochilodus magdalenae*].—Vari and Howe, 1991:34 [holotype depository].

Prochilodus magdalenensis.—Posada Arango, 1909:300 [Río Magdalena, unjustified emendation of species name].

Prochilodus steindachneri Eigenmann, 1920b:16 [nomen nudum; cited from Río Magdalena basin].

Prochilodus steindachneri Eigenmann, 1922a:115 [type locality: Cauca near Caceres (=Colombia, Antióquia, Río Cauca, close to Cáceres); preoccupied by *Prochilodus steindachneri* Fowler, 1906 (=*Prochilodus vimboides* Kner, 1859) and replaced by *Prochilodus eigenmanni* Ahl, 1937].

Prochilodus asper magdalenae.—Eigenmann, 1922a:114 [cited in synonymy of *Prochilodus magdalenae* Steindachner, 1879a].

Prochilodus eigenmanni Ahl, 1937:136 [type locality: Colombia, Antióquia, Río Cauca, close to Cáceres; name proposed as substitute for *Prochilodus steindachneri* Eigenmann, 1922, that was preoccupied by *Prochilodus steindachneri* Fowler, 1906].—Fowler, 1942:133 [Colombia, Río Cauca]; 1975:358 [literature compilation].

Prochilodus reticulatus magdalenae.—Schultz, 1944:261 [shift of *Prochilodus asper* var. *magdalenae* Steindachner (1879a) to subspecies of *P. reticulatus*].—Dahl, 1955:17 [Colombia, Río Sinu; economic importance]; 1963a:43 [Colombia, Ríos Magdalena, Sinú, Atrato; economic importance; common name]; 1963b:95 [habitat, reproduction]; 1971:xvi, 109, text figure [Colombia, Río Magdalena and Río Sinú; major economic importance; life history].—Henao, 1963:57 [life history].—Dahl and Medem, 1964:55 [Colombia, Rio Sinu].—Patiño R., 1973:79, fig. 29 [Colombia, Río Magdalena-Cauca basin, Río San Jorge, Río Atrato, Río Sinú; commercial importance, life history, and ecology].—Fowler, 1975:360 [literature compilation].—Godoy, 1975:67 [economic importance].—Flórez, 1985:9 [Río Magdalena system; ecology].—Petrere, 1985:10 [importance in fisheries].

Prochilodus sp.—Román-Valencia, 1990:204 [Colombia, middle Río Atrato].

DIAGNOSIS.—*Prochilodus magdalenae* differs from *P. brevis, P. lacustris, P. mariae, P. nigricans,* and *P. rubrotaeniatus* in the lack of dark, irregular, wavy, bar-like patterns on the caudal-fin lobes that are present in those five species. Within the group of *Prochilodus* species that lack dark caudal-fin markings, *P. magdalenae* differs from *P. vimboides* in the number of scales along the lateral line (43 to 46 versus 34 to 39, respectively), the number of horizontal rows of scales between the dorsal-fin origin and the lateral line (8 or 9 versus 5 to 7, respectively), and the number of horizontal rows of scales around the caudal peduncle (17 to 19 versus 13 to 15, respectively); from *P. britskii* in the number of scales between the dorsal-fin origin and the lateral line (8 or 9 versus 6 or 7, respectively), the number of horizontal rows of scales around the caudal peduncle (17 to 19 versus 13 or 14, respectively), and the number of teeth in the inner row of each side of the lower jaw (9 to 16 versus 6 or 7, respectively); from *P. hartii* in the lack of a series of wavy stripes along the lateral surface of the body (versus the presence of such stripes in all but largest specimens examined), the number of horizontal rows of scales around the caudal peduncle (17 to 19 versus 14 to 16, respectively), and the number of scales along the lateral line (43 to 46, 44 most frequent, versus 40 to 43, 41 most frequent, respectively); from *P. argenteus* in the number of horizontal rows of scales between the dorsal-fin origin and the lateral line (8 or 9 versus 10 or 11, respectively) and in the number of vertebrae (39 to 42 versus 42 to 44, respectively); from *P. lineatus* in the absence of the series of wavy dark stripes along the body (versus presence of such stripes in *P. lineatus*) and in the number of vertebrae (39 to 41 versus 42 to 44); from *P. costatus* in the absence of the series of wavy dark stripes along the body (versus presence of such stripes in *P. costatus*) and in the number of vertebrae (39 to 41 versus 41 to 43, with 41 in only 1 of 6 specimens radiographed, respectively); and from *P. reticulatus* in the ranges and modal values of the number of scales along the lateral line (43 to 46, 44 and 45 most frequent, versus 41 to 45, 42 and 43 most frequent and 45 present in only 1 specimen examined for this feature, respectively; Figure 48), the number of vertebrae (39 to 42 with 41 most frequent and 39 in only 8.1% of radiographed specimens versus 38 to 40 with 39 most frequent and 40 present in only 11.1% of radiographed specimens, respectively, Figure 49), and the number of median predorsal scales (12 to 17, with 13 most frequent, versus 11 to 18 with 15 and 16 most frequent, respectively; Figure 50).

DESCRIPTION.—Morphometric and meristic data for *Prochilodus magdalenae* presented in Table 12. Body moderately high, transversely compressed. Greatest body depth at dorsal-fin origin. Dorsal profile of head ranging from gently concave to straight. Predorsal profile of body moderately convex. Body profile posteroventrally inclined along dorsal-fin

TABLE 12.—Morphometrics and meristics of *Prochilodus magdalenae:* (A) lectotype of *Prochilodus asper* var. *magdalenae,* NMW 56627:1; (B) paralectotypes of *Prochilodus asper* var. *magdalenae,* NMW 56624–26, NMW 56628; (C) holotype of *Prochilodus beani,* USNM 1662; (D) paratype of *Prochilodus beani,* USNM 306593; (E) holotype of *Prochilodus eigenmanni,* NMW 68274; and (F) all specimens of *Prochilodus magdalenae* from which counts and measurements were taken. Standard length is presented in mm; values 2 to 16 are percentages of SL, 17 to 21 are percentages of HL; dash indicates unobtainable datum, and question mark indicates specimen damaged for the indicated feature.

Characters	A	B	C	D	E	F
			Morphometrics			
1. Standard length	234.4	130.0–296.2	155.8	149.0	218.9	46.4–312.0
2. Greatest body depth	32.1	32.3–35.0	33.8	37.9	34.8	29.4–38.6
3. Predorsal length	43.7	42.1–46.1	45.3	45.2	45.2	42.1–47.3
4. Dorsal-fin base length	17.9	17.7–18.9	19.9	19.4	17.9	15.7–20.5
5. Dorsal fin to adipose fin distance	26.1	25.9–27.9	27.0	25.3	24.3	23.3–29.6
6. Dorsal fin to caudal fin distance	42.4	41.7–45.6	42.7	41.1	43.0	40.2–45.6
7. Prepelvic length	47.5	46.2–49.8	49.6	50.1	49.0	46.2–51.5
8. Preanal distance	73.4	68.8–73.8	75.5	75.6	74.1	68.8–77.7
9. Snout to anal-fin insertion	76.8	74.8–78.7	79.9	79.6	76.5	74.3–80.0
10. Anal-fin base length	9.9	11.1–12.0	12.1	13.1	11.8	9.3–13.3
11. Caudal-peduncle length	15.5	14.9–16.8	11.7	13.4	14.9	11.7–16.8
12. Dorsal-fin length	30.4	28.2–32.4	32.5	32.6	30.0	26.7–35.5
13. Pectoral-fin length	22.1	20.1–23.4	22.6	23.2	21.2	20.1–24.9
14. Pelvic-fin length	21.5	19.9–21.2	20.3	21.9	20.5	18.0–23.6
15. Least caudal-peduncle height	12.5	11.6–12.4	11.4	11.9	11.9	9.7–12.5
16. Head length	25.3	25.1–41.7	28.4	27.4	27.0	25.1–30.9
17. Snout length	38.7	35.4–41.7	39.5	38.0	34.5	33.2–41.7
18. Bony orbital diameter	19.6	18.8–24.4	23.9	24.5	21.8	17.8–28.9
19. Postorbital length	46.5	42.7–47.4	41.3	40.2	47.6	38.5–48.1
20. Interorbital width	54.2	53.3–57.6	53.4	53.4	53.7	48.2–57.6
21. Mouth width	44.3	41.4–46.8	42.2	45.3	39.2	37.2–49.0
			Meristics			
Lateral-line scales	45	44–45	44	44	45	43–46
Scale rows between dorsal-fin origin and lateral line	9	8–9	9	9	8	8–9
Scale rows between anal-fin origin and lateral line	7	6–7	7	7	7	6–7
Scale rows between pelvic-fin insertion and lateral line	8	7–8	8	8	8	7–8
Rows of scales around caudal peduncle	19	18–19	18	18	18	17–19
Median predorsal scales	16	14–16	14	13	16	12–17
Median scales between dorsal and adipose fins	16	15–16	15	15	16	13–16
Vertebrae	40	–	40	40	41	39–42
Inner row teeth, upper jaw	20	16–21	20	15	19?	15–23
Inner row teeth, lower jaw	12	11–16	11	9	11	9–16

base; profile ranging from gently convex to straight from posterior of dorsal-fin base to adipose-fin origin, and concave along caudal peduncle. Predorsal portion of body with slight median ridge. Postdorsal region of body transversely obtusely rounded. Ventral profile of body moderately convex from tip of lower jaw to posterior of anal-fin base. Ventral profile of caudal peduncle concave. Prepelvic region transversely flattened proximate to pelvic-fin insertion. Distinct median keel present between pelvic-fin insertion and anus.

Head profile pointed. Snout length greater than horizontal width of orbit. Nares of each side of head close to each other; anterior nares circular, posterior nares crescent shaped. Adipose eyelid present but poorly developed; most developed anteriorly, but with greater part of eye uncovered. Lips fleshy and forming oral disk when protracted.

Functional teeth in two rows in each jaw. All teeth movably implanted in flesh that overlies jaws. All teeth of similar size, with exposed portion spoon shaped except when worn down. Inner tooth series in each jaw of protracted mouth with 15 to 23 teeth on left side of upper jaw and 9 to 16 teeth on left side of lower jaw. Outer row of teeth in each jaw with approximately 72 teeth on each side of upper jaw and approximately 57 teeth on each side of lower jaw in the lectotype. Upper and lower lips bordered by numerous globular, fleshy papillae.

Scales spinoid. Scales in middorsal series between posterior of dorsal-fin base and adipose-fin origin similar in form to those of adjoining regions of body. Lateral line with 43 to 46 (40% of specimens with 45) pored scales; 8 or 9 (65.1% of specimens with 9) horizontal rows of scales between dorsal-fin origin and lateral line; 7 or 8 (57.1% of specimens with 8) horizontal rows of scales between pelvic-fin insertion and lateral line; 6 or 7 (60.5% of specimens with 7) horizontal rows of

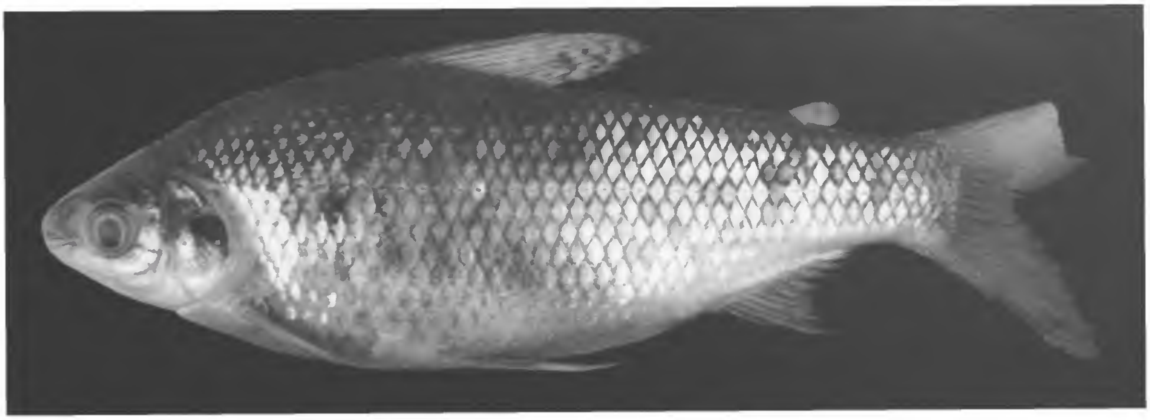


FIGURE 47.—*Prochilodus magdalenae*, MZUSP 36690, 184.4 mm SL; Colombia, Huila, ciénega La Bija, near San Pabló, Río Magdalena.

scales between anal-fin origin and lateral line; 12 to 17 (54.2% of specimens with 16 or 17) median predorsal scales; 13 to 16 (35.7% of specimens with 15) scales in middorsal series between posterior of dorsal-fin base and adipose-fin origin; 17 to 19 (83.3% of specimens with 18) horizontal rows of scales around caudal peduncle.

Dorsal fin preceded by small, but well-developed, anteroventrally bifurcate, procumbent spine somewhat triangular in lateral view. Dorsal-fin rays (including procumbent spine) iii,10 [iii,10]; anal-fin rays iii,8 or 9 (iii,8 most frequent) [iii,8]; pectoral-fin rays i,12 to 17 (i,15 most frequent) [i,14]; pelvic-fin rays i,8 or 9 (i,8 most frequent) [i,8]; principal caudal-fin rays 10/9 [10/9].

Vertebrae 39 to 42 (44.1% of specimens with 41).

Dorsal fin truncate, slightly pointed distally; posterior unbranched and anterior branched rays longest and subequal. Dorsal-fin origin located closer to tip of snout than to caudal-fin base. Greatest length of adipose fin approximately equal to horizontal width of orbit. Adipose-fin origin located along vertical that passes approximately through posterior one-third of anal-fin base. Pectoral fin distally pointed. Tip of adpressed pectoral fin reaching posteriorly approximately four-fifths of distance between pectoral-fin and pelvic-fin insertions. Pelvic fin falcate. Pelvic-fin insertion located slightly posterior to vertical that passes through dorsal-fin origin. Tip of adpressed pelvic fin reaching posteriorly approximately four-fifths of distance between pelvic-fin insertion and anus. Axillary scale present, its length approximately one-third of greatest length of pelvic fin. Posterior unbranched and anterior branched anal-fin rays longest and subequal. Caudal fin bifurcate.

COLORATION IN ALCOHOL—Ground coloration silvery yellow or brownish yellow, with dorsal portion of body and head darker. Lateral surface of body with up to 10 dark, diffuse, vertical, irregular patches of pigmentation between head and caudal fin. Patches with approximate overall form of narrow isosceles triangles, with apexes positioned along middle of ventrolateral surface of body and bases along dorsomedial region of body. Patches obvious in small specimens, but indistinct or absent in large individuals. Lateral surface of body lacking distinct dark, wavy, horizontal stripes present in many congeners. Field of brown or black chromatophores forming dark, irregular patch on upper one-half of opercle.

Dorsal fin with 5 to 10 (most frequently 6) dark, irregular stripes beginning on anterior margin of fin and running approximately parallel to dorsal-fin base. Adipose fin with small, dark, diffuse marks and with border finely marked with black. Pectoral, pelvic, anal, and caudal fins dusky. Iris yellowish silver, with diffuse dusky areas on dorsal and ventral portions.

DISTRIBUTION.—Examined specimens of *Prochilodus magdalenae* originated in the Río Atrato, Río Sinú, and Río Cauca-Magdalena basins in northwestern Colombia (Figure 43, squares). In addition, Mojica-C. (1995:554) cited *P. magdalenae* from the Río Rancheria, an independent coastal drainage in the state of Guajira, on the Peninsula of Guajira, Colombia (approximately 11°34'N, 72°54'W).

COMMON NAME.—Bocachico (Colombia).

COMPARISONS.—Meristic features and details of pigmentation unequivocally distinguish *Prochilodus magdalenae* from all of its congeners with the exception of *P. reticulatus*, the only other member of the genus with a Trans-Andean distribution. The two nominal forms differ in the ranges for the number of scales along the lateral line and in the number of vertebrae, and they differ in the modal value for the number of predorsal scales (see details in "Diagnosis," above, and Figures 48–50). In light of these differences and the geographic separation of their areas of occurrence, we treat these nominal forms as separate species herein.

ECOLOGY AND REPRODUCTION.—According to Patiño R. (1973:79), *Prochilodus reticulatus magdalenae* (the *P. magdalenae* of this study) was historically the most important and

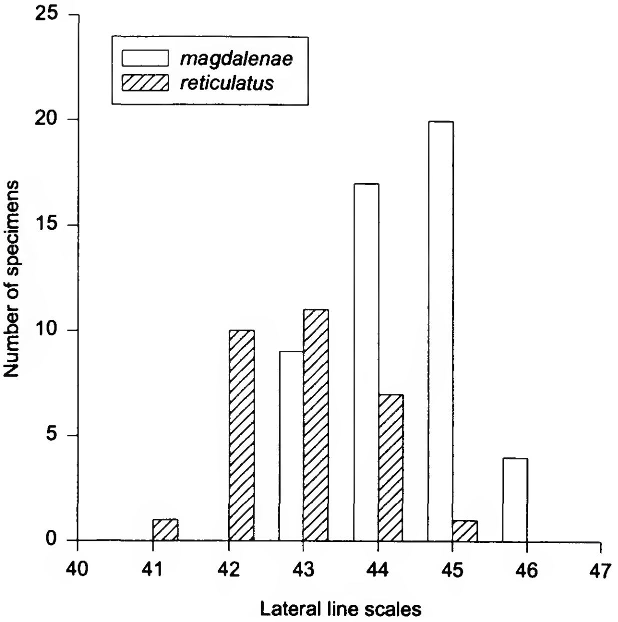


FIGURE 48.—Histogram of number of lateral-line scales plotted against number of specimens with particular counts in *Prochilodus magdalenae* and *Prochilodus reticulatus*.

valued species in the freshwater fisheries of Colombia, accounting for approximately 50% of the catch. That author reported that populations of *P. magdalenae* have been adversely affected by habitat destruction resulting from direct and indirect anthropogenic activities and as a consequence of competition from introduced species. The majority of its yearly cycle is spent in lentic waters, but during the breeding season it undergoes an upriver migration to its spawning grounds. The larvae move downstream with the rains to return to quiet backwaters where they develop and mature. Sánchez et al. (2000:218–219) reported that *P. magdalenae* is one of the most important commercial fish species in the upper Río Magdalena basin below the Betania impoundment.

REMARKS.—Steindachner's (1879a:51–53, pl. 11: fig. 1, 1a) description of *Prochilodus asper* var. *magdalenae* was based upon a series of specimens that originated in the Río Magdalena drainage system of Colombia. We herein designate NMW 56627:1 (234.4 mm SL), the syntype in the best condition, as the lectotype of the species. The remaining syntypes (NMW 56627:2–3, 265.4–276.0 mm SL; NMW 56624, 4 specimens, 206.2–294.2 mm SL; NMW 56625, 5 specimens, 130.0–161.8 mm SL; NMW 56626, 2 specimens, 253.8–264.0 mm SL; and NMW 56628, 3 specimens, 236.3–296.2 mm SL) consequently become paralectotypes.

Although Steindachner (1879a:51) proposed *Prochilodus asper* var. *magdalenae* for Colombian populations of the genus, that author subsequently (1880:67; 1902:141) reported on the *Prochilodus* populations from northwestern Colombia as *P. asper*, without comment as to this change in nomenclature. As discussed under *P. reticulatus*, *P. asper* is a synonym of *P. reticulatus*—a species endemic to the Lago Maracaibo basin of northeastern Colombia and northwestern Venezuela. As such, we utilize *P. magdalenae* for the *Prochilodus* populations in the Río Magdalena system and adjoining drainages in northwestern Colombia.

Steindachner (1880:68–69) questionably identified a specimen of *Prochilodus* that originated in the Río Cauca of northwestern Colombia as *P. rubrotaeniatus*. Our results indicate that *P. rubrotaeniatus* has an entirely Cis-Andean distribution and indeed occurs only in the Guianas, the Río Caroni, and the Río Negro basins, regions far distant from the Río Cauca. In his treatment of the members of the Prochilodontidae in western South America, Eigenmann (1922a:115–116) apparently did not examine the specimen reported on by Steindachner (1880) as *P. rubrotaeniatus*. He further specifically noted that "no specimens of this species were secured" and continued on that "it [*P. rubrotaeniatus*] may be merely a variety of *P. magdalenae*." Despite being unable to examine any specimens of this putative form and his uncertainty as to its distinctiveness, Eigenmann (1922a:115–116) nonetheless proposed a new species, *Prochilodus steindachneri*. The description of *Prochilodus steindachneri* was based upon the individual from the Río Cauca that had been questionably identified by Steindachner (1880) as *P. rubrotaeniatus*. The name proposed by Eigenmann (1922a), *P. steindachneri*, was, however, preoccupied by *P. steindachneri* Fowler, 1906 (=*P. vimboides;* see under synon-

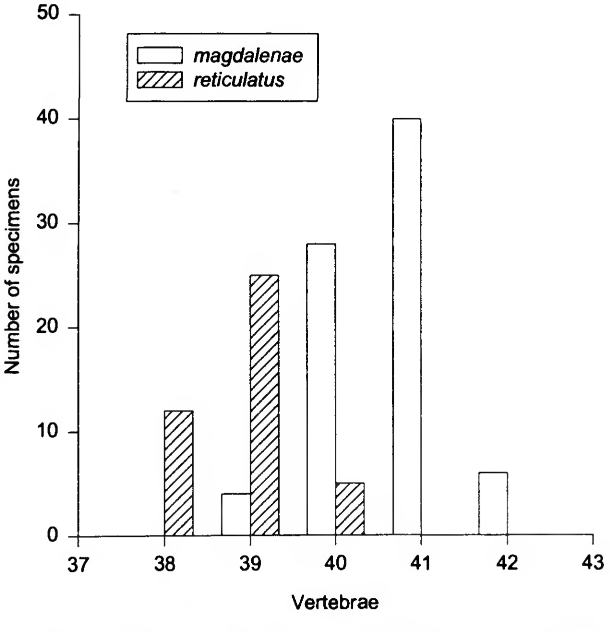


FIGURE 49.—Histogram of number of vertebrae plotted against number of specimens with particular counts in *Prochilodus magdalenae* and *Prochilodus reticulatus*.

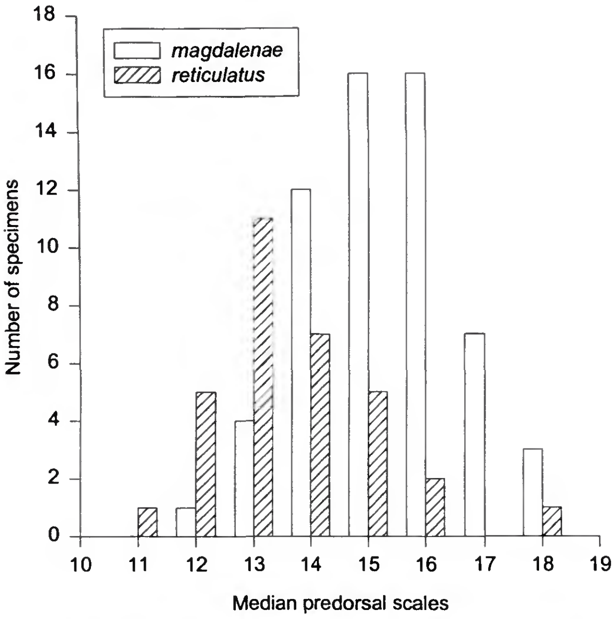


FIGURE 50.—Histogram of number of median predorsal scales plotted against number of specimens with particular counts in *Prochilodus magdalenae* and *Prochilodus reticulatus*.

ymy of the latter species). In order to rectify that problem, Ahl (1937:136) proposed *Prochilodus eigenmanni* as a replacement name for *P. steindachneri* of Eigenmann (1922). As shown in Table 12, no differences were found in examined body systems between the holotype of *P. eigenmanni* and examined samples of *P. magdalenae*. *Prochilodus eigenmanni* is consequently herein considered to be a junior synonym of *P. magdalenae*, a finding in agreement with Eigenmann's (1922a: 116) original tentative supposition.

Prochilodus beani was described by Eigenmann (in Eigenmann and Ogle, 1907:5, fig. 2) from two specimens that originated at Truandó in the Río Atrato basin of northwestern Colombia. In his comments in the description of this species, Eigenmann noted that *P. beani* was "allied to *brevis, rubrotaeniatus, cephalotes, magdalenae, argenteus, platensis,* and *scrofa*" but did not contrast his new species with *P. magdalenae* that had been already described from the adjoining Río Magdalena system of Colombia. Rather, Eigenmann limited his comparisons of *P. beani* to *P. scrofa*, a nominal species of eastern Brazil that is herein considered to be a synonym of *P. lineatus*. Reference to Table 12 demonstrates that *P. beani* falls within the range of variation for *P. magdalenae* in all meristic and morphometric features examined in this study, and the two nominal forms agree in all other examined attributes. As a consequence, *P. beani* is herein considered to be a junior synonym of *P. magdalenae*.

Without discussion of the basis for his action, Schultz (1944:261–264) placed *Prochilodus magdalenae*, herein considered to be endemic to the Río Atrato, Río Sinú, and Río Cauca-Magdalena of Colombia, as a subspecies of *P. reticulatus*, a species considered, in this paper, to be endemic to Lago Maracaibo of northwestern Venezuela and northeastern Colombia. This action is puzzling in so far as the data in Schultz' publication (1944, table 7) shows non-overlapping values in the ranges of lateral-line scale counts between what he recognized to be two subspecies (*P. reticulatus reticulatus* and *P. r. magdalenae*). Our results fail to demonstrate such trenchant differences between what Schultz (1944) recognized as *P. r. reticulatus* and *P. r. magdalenae*. Nonetheless, the samples of *Prochilodus* from the Río Atrato, Río Sinú, and Río Cauca-Magdalena, on the one hand, and those from the Lago Maracaibo basin, on the other, differ in the modal values and ranges for the number of scales along the lateral line and in the number of vertebrae, albeit with partial overlap for these features. They also have nearly complete overlap in the number of scales in the median predorsal series, but they have distinctly different average and modal values for that feature (Figures 48 to 50; see also "Diagnosis" for details of the differences between the two forms). Because of those differences and the complete geographic separation of the forms, we recognize *P. reticulatus* and *P. magdalenae* to be distinct species in this study.

MATERIAL EXAMINED.—204 specimens (41, 46.4–312.0 mm SL; partial meristic data taken from an additional 47 specimens).

COLOMBIA. *Antioquia:* "Ciénega" (= floodplain marsh or pool) of Río Magdalena, near Puerto Berrío, CAS 18318 (formerly IU 13046), 2 (1, 166.3–312.0). Puerto Berrío, CAS 58987 (formerly IU 12887), 1 (1, 125.6) [1R]; CAS 58988 (formerly IU 12888), 1 (116.1) [1R]. Peñas Blancas, CAS 11630 (formerly IU 12811), 5 (1, 102.1–251.0) [1R]. Río Cauca, near Cáceres, NMW 68274, 1 (1, 218.9, holotype of *Prochilodus eigenmanni*) [1R]. *Atlântico:* Barranquilla, BMNH 1900.1.30:25-7, 3 (1, 92.5–155.8) [1R]. *Bolivar:* Soplaviento, CAS 18374 (formerly IU 12886), 1 (1, 61.7). Calamar, Río Magdalena, CAS 11624 (formerly IU 12885), 13 (1, 46.4–242.0) [1R]; USNM 79231, 3 (92.6–115.4) [3R]. *Caldas:* Caño Aguas Negras, 5.3 km by road downstream of San Miguel, ANSP 128132, 1 (1, 289.4). Río Miel, Hacienda Sonadora, approximately 8 km downstream of San Miguel, ANSP 128131, 1 (1, 272.6). *Cauca:* Río Cauca basin, Timba (3°07′N, 76°37′W), NRM 24961, 2; NRM 24962, 3. *Chocó:* Río Truandó, AMNH 5344, 9 (1, 100.5–207.9) [1R]; CAS 22752 (formerly IU 13578), 5 (1, 118.1–127.6) [1R]; CAS 58985 (formerly IU 13578), 19 (1, 78.5–162.8) [1R]; CAS 59346, 10 (1, 101.6–165.7) [1R]; UMMZ 197556, 6 (1, 100.5–110.2) [1R]; USNM 1662, 1 (1, 155.8, holotype of *Prochilodus beani*) [1R]; USNM 76962, 17 (1, 88.5–138.5) [17R]; USNM 306593, 1 (1, 149.0, paratype of *Prochilodus beani*, formerly USNM 1662a) [1R]. Río Salado, approximately 1 mi [1.6 km] upriver of confluence with Río Truando, USNM 290140, 2 (173.5–179.5). Río Salado, approximately 4 mi [6.4 km] upriver of confluence with Río Truandó, USNM 220200, 2 (1, 116.0–117.0) [2R]; USNM 290139, 14 (118.8–132.3) [14R]; USNM 290142, 2 (287.6–300.0). Río Salado, approximately 0.25 mi [0.4 km] upriver of confluence with Río Truandó, USNM 290141, 3 (142.0–167.6) [3R]. Río Pavavando, tributary of Río Salaqui, USNM 290143, 2 (129.0–150.6) [2R]. Río Salado, near Teruita, USNM 290144, 7 (152.0–231.2) [3R]. Quibdó, Río Atrato, CAS 59347 (formerly IU 13044), 3 (1, 94.3–251.5) [1R]; CAS 59348 (formerly IU 12809), 1 (246.3) [7R]. Río Atrato, near city of Río Sucio, USNM 321671, 4 (201.0–257.0) [1R]. Río Sucio, Río Sucio, AMNH 8735, 1 (271.8); CAS 11592 (formerly IU 12810), 3 (1, 237.2–242.3) [1R]; USNM 79251, 3 (1, 254.1–265.9). Río Atrato basin, mouth of Río Bojayá, at Bellavista, NRM 30726, 1. Río Atrato basin, Napipí, Ciénega Napipí, NRM 30728, 1. *Córdoba:* Lorica, Río Sinú, CAS 06408, 1 (232.8) [1R]. *Cundinamarca:* Apulo, CAS 11585, 4 (1, 239.5–251.6) [1R]; CAS 11629 (formerly IU 13043), 2 (1, 211.9–234.0) [1R]. Girardot, CAS 59349 (formerly IU 12889), 2 (1, 177.2–281.4) [1R]. *Huila:* Ciénega La Bija, Río Mag-dalena, near San Pabló, MZUSP 36690, 4 (184.4–196.4). *Magdalena:* Ciénega, Río Magdalena, NMW 56624, 4 (1, 206.2–294.2, paralectotypes of *Prochilodus asper* var. *magdalenae*); NMW 56625, 5 (1, 130.0–161.8, paralectotypes of *Prochilodus asper* var. *magdalenae*); NMW 56626, 2 (1, 253.8–264.0, paralectotypes of *Prochilodus asper* var. *magdalenae*) [1R]; NMW 56627:1, 1 (1, 234.4, lectotype of *Prochilodus asper* var. *magdalenae*) [1R]; NMW 56627: 2–3, 2 (265.4–276.0, paralectotypes of *Prochilodus asper* var. *magdalenae*) [2R]; NMW 56628, 3 (1, 236.3–296.2, paralectotypes of *Prochilodus asper* var. *magdalenae*) [1R]. Río Magdalena, NMW 56629:1-2, 2 (1, 237.2–269.1); NMW 56630, 1 (276.3); NMW 56631, 1 (approximately 240 mm SL); NMW 56632, 1 (279.9). *Tolima:* Piedra Moler, CAS 59351 (formerly IU 12890), 2 (1, 196.6–288.6) [1R]. Honda, Río Magdalena, CAS 18496 (formerly IU 12891), 1 (205.9) [1R]; UMMZ 191064, 1 (241.5) [1R]. *Valle:* Paila, CAS 58986 (formerly IU 12892), 4 (1, 134.1–160.6) [1R]. Buga Valle, Río Media Caños, UMMZ 191065, 1 (181.0) [1R]. *Inexact Locality:* Río Magdalena, MNHN 2374, 4 (1, 151.8–233.2). Soplaviento or Honda, CAS 18309 (formerly IU 12886 or 12891), 2 (1, 245.2–252.2).

***Prochilodus mariae* Eigenmann, 1922**

FIGURES 51, 52; TABLE 13

Prochilodus brama [not of Valenciennes, 1850].—Peters, 1877:472 [Venezuela, Calabozo].—Eigenmann, 1910:424 [in part, Río Orinoco citation]; 1912:67 [Río Orinoco basin].

Prochilodus mariae Eigenmann, 1922a:231 [type locality: Barrigón, Río Meta (=Colombia, Río Meta, Barrigón)]; 1922b:163 [Spanish version of Eigenmann, 1922a].—Fowler, 1942:133 [Colombia, Río Meta].—Mago-Leccia, 1970:31 [Venezuela]; 1972:48, figs. 5a, 6 [redescription, Río Orinoco basin]; 1978:15 [Venezuela].—Cala, 1977:9 [Colombia, eastern llanos, Río Meta].—Géry, 1977:219 [Río Orinoco].—Novoa R. et al., 1982:276 [Venezuela, Río Orinoco; life history information, major importance in fisheries].—Saldaña and Venables, 1983:617 [migration, energy compartmentalization].—Lowe-McConnell, 1984:143 [economic importance].—Taphorn and Lilyestrom, 1984b:70 [Venezuela, Apure].—Flórez, 1985:9 [Colombia, Río Metica].—Machado-Allison, 1987:25 [Venezuelan llanos]; 1992:48 [larval ecology, Río Orinoco basin].—Machado-Allison et al., 1987:134 [Venezuela, natural history, llanos]; 1990:414 [Venezuela, ecology].—Lasso, 1988:133 [lower Río Orinoco]; 1992:15 [Venezuela, Río Suapure; ecology].—Menezes and Vazzoler, 1992:62 [reproductive characteristics].—Taphorn 1992:483 [Venezuela, Río Apure basin; life history].—Balbás and Taphorn, 1996:78 [Venezuela, Río Caura].—Flecker 1996:1845 [Venezuela; importance in determining community structure and ecosystem attributes].—Winemiller et al., 1996:38, fig. 5a [Venezuela; economic importance; deleterious impact of human activities on populations].—Taphorn et al., 1997:79 [Venezuela].—Barbarino Duque et al., 1998:33 [deleterious impacts of impoundments and over fishing on populations of *P. mariae* in western Venezuela].—Machado-Allison et al., 1999:66 [Venezuela, Río Caura basin].—Mojica-C., 1999:554 [Colombia, Río Orinoco, Río Inirida, Río Guaviare, Río Cusiana, Río Meta, Río Arauca].—Ponte J. et al., 1999:42 [Venezuela, delta of Río Orinoco].

(?) *Prochilodus asper* [not of Lütken, 1875].—Fernández-Yépez, 1969:55 [Venezuela, Río Caroni].

DIAGNOSIS.—The dark, irregular, wavy, bar-like patterns on the caudal-fin lobes in *Prochilodus mariae* discriminates that species from *P. argenteus*, *P. britskii*, *P. costatus*, *P. hartii*, *P. lineatus*, *P. magdalenae*, *P. reticulatus*, and *P. vimboides*, which have hyaline caudal fins. *Prochilodus mariae* is distinguished from all of its congeners that also have irregular, dark caudal-fin bars (*P. brevis*, *P. lacustris*, *P. nigricans*, *P. rubrotaeniatus*) by the number of scales along the lateral line (52 to 64, 52 in only 1 of 39 specimens examined for this feature, versus 41 to 51 in those four species in combination, with 51 in only 2 of 50 specimens of *P. lacustris* of northeastern Brazil examined for this feature, respectively). *Prochilodus mariae* further differs from *P. lacustris* in the number of rows of dark, wavy, horizontal stripes ventral of the lateral line (6 or 7 versus 7 to 10, respectively) and in the mode and the number of median scales between the posterior of the dorsal-fin base and the adipose-fin origin (17 to 23, 18 and 19 most frequent, versus 14 to 18, 16 most frequent, respectively).

DESCRIPTION.–Morphometric and meristic data for *Prochilodus mariae* presented in Table 13. Body comparatively high, transversely compressed. Greatest body depth at dorsal-fin origin. Dorsal profile of head gently concave. Predorsal profile of body convex. Body profile posteroventrally inclined along dorsal-fin base; straight from posterior of dorsal-fin base to adipose-fin origin, and concave along caudal peduncle. Predorsal portion of body with slight median ridge. Postdorsal portion of body obtusely rounded transversely. Ventral profile of body moderately convex from tip of lower jaw to posterior of anal-fin base. Ventral profile of caudal peduncle concave. Prepelvic region of body transversely flattened proximate to pelvic-fin insertion. Distinct midventral keel present between pelvic-fin insertion and anus.

Head profile pointed. Mouth terminal. Snout length greater than horizontal width of orbit. Nares of each side of head close to each other; anterior nares circular, posterior nares crescent shaped. Adipose eyelid present but poorly developed; most developed anteriorly, but with greater part of eye uncovered. Lips fleshy, moderately developed relative to those in some other prochilodontids, and forming oral disk when protracted.

TABLE 13.—Morphometrics and meristics of *Prochilodus mariae:* (A) holotype of *Prochilodus mariae,* CAS 15150; (B) paratype of *Prochilodus mariae,* CAS 23942; and (C) all specimens of *Prochilodus mariae* from which counts and measurements were taken. Standard length is presented in mm; values 2 to 16 are percentages of SL, 17 to 21 are percentages of HL.

Characters	A	B	C
		Morphometrics	
1. Standard length	234.0	225.6	29.6–366.5
2. Greatest body depth	34.9	35.9	29.0–42.6
3. Predorsal length	48.2	46.3	42.9–50.7
4. Dorsal-fin base length	16.8	18.5	16.4–19.9
5. Dorsal fin to adipose fin distance	27.1	27.7	21.3–30.2
6. Dorsal fin to caudal fin distance	42.6	44.1	37.8–46.4
7. Prepelvic length	51.3	49.4	47.6–56.3
8. Preanal distance	76.5	74.0	74.0–81.2
9. Snout to anal-fin insertion	82.0	80.9	78.7–85.2
10. Anal-fin base length	12.1	13.0	9.2–13.9
11. Caudal-peduncle length	11.7	12.6	11.5–14.5
12. Dorsal-fin length	29.9	31.5	24.6–39.9
13. Pectoral-fin length	22.1	22.8	16.2–25.0
14. Pelvic-fin length	21.5	22.0	13.3–24.6
15. Least caudal-peduncle height	12.3	12.3	11.0–14.2
16. Head length	27.0	27.2	24.6–32.4
17. Snout length	45.2	44.4	35.2–53.6
18. Bony orbital diameter	20.9	21.0	17.7–34.6
19. Postorbital length	41.2	40.1	36.4–44.4
20. Interorbital width	54.0	55.5	52.4–62.3
21. Mouth width	46.6	45.8	43.2–52.0
		Meristics	
Lateral-line scales	53	61	52–64
Scale rows between dorsal-fin origin and lateral line	10	11	10–11
Scale rows between anal-fin origin and lateral line	7	7	7–8
Scale rows between pelvic-fin insertion and lateral line	9	9	8–10
Rows of scales around caudal peduncle	18	18	17–19
Median predorsal scales	21	20	17–22
Median scales between dorsal and adipose fins	18	18	17–23
Vertebrae	42	41	40–42
Inner row teeth, upper jaw	22	22	15–25
Inner row teeth, lower jaw	13	13	8–14

Functional teeth in two rows in each jaw. All teeth movably implanted in flesh that overlies jaws. All teeth of similar size, with exposed portions spoon shaped except when worn down. Inner tooth series in each jaw with 15 to 25 teeth on left side of upper jaw and 8 to 14 teeth on left side of lower jaw. Outer row of teeth in each jaw with approximately 100 teeth on each side of upper jaw and approximately 89 teeth on each side of lower jaw in holotype. Upper and lower lips bordered by numerous globular, fleshy, papillae.

Scales spinoid. Scales in middorsal series between posterior of dorsal-fin base and adipose-fin origin similar in form to those of adjoining regions of body. Lateral line with 52 to 64 (25.6% of specimens with either 58 or 59) pored scales; 10 or 11 (66.7% of specimens with 11) horizontal rows of scales between dorsal-fin origin and lateral line; 8 to 10 (71.8% of specimens with 9) horizontal rows of scales between pelvic-fin insertion and lateral line; 7 or 8 (71.8% of specimens with 7) horizontal rows of scales between anal-fin origin and lateral line; 17 to 22 (22.2% of specimens with 21) median predorsal scales; 17 to 23 (59.4 specimens with either 18 or 19) scales in middorsal series between posterior of dorsal-fin base and adipose-fin origin; 17 to 19 (84.6% of specimens with 18) horizontal rows of scales around caudal peduncle.

Dorsal fin preceded by small, but well-developed, anteroventrally bifurcate, procumbent spine somewhat triangular in lateral view. Dorsal-fin rays (including procumbent spine) iii,10 [iii,10]; anal-fin rays iii,7 or 8, or ii,7 (iii,8 most frequent) [iii,8]; pectoral-fin rays i,12 to 17 (i,15 most frequent) [i,16]; pelvic-fin rays i,8 [i,8]; principal caudal-fin rays 10/9 [10/9].

Vertebrae 40 to 42 (75.0% of specimens with 41).

Dorsal fin truncate and slightly pointed distally; posterior unbranched and anterior branched longest and subequal. Dorsal-fin origin located closer to tip of snout than to caudal-fin base. Greatest length of adipose fin approximately equal to horizontal width of orbit. Adipose-fin origin situated along vertical that passes through anterior one-third of anal-fin base. Pectoral fin pointed distally. Tip of adpressed pectoral fin reaching posteriorly to, or almost to, pelvic-fin insertion. Pelvic fin falcate. Pelvic-fin insertion located along vertical that passes approximately through middle of dorsal-fin base. Tip of adpressed pelvic fin reaching posteriorly approximately four-fifths of distance between pelvic-fin insertion and anus. Axillary scale present, its length approximately one-fourth of greatest length of pelvic fin. Posterior unbranched and anterior branched anal-fin rays longest and subequal. Caudal fin moderately bifurcate.

COLORATION IN ALCOHOL.—Ground coloration silvery yellow or brownish yellow, with dorsal portion of body and head darker. Lateral portion of body typically with 10 to 16 vertical, diffuse, and irregular patches of dark pigmentation between head and caudal fin. Patches with approximate overall form of narrow isosceles triangles with apexes positioned along middle of ventrolateral portion of body and bases along dorsomedial region. Patches well developed in smaller specimens, but indistinct or absent in larger individuals. Lateral surface of body with approximately 12 to 14 dark, wavy, horizontal stripes along dorsal and ventral margins of exposed portions of scales. Approximately 6 or 7 wavy stripes dorsal to, and 6 or 7 wavy lines ventral to, lateral line. Field of black or brown chromatophores forming dark, irregular mark on dorsal one-half of opercle.

Dorsal fin with 5 to 7 (most frequently 5) irregular dark stripes beginning at anterior margin and extending across fin approximately parallel to base of fin. Adipose fin with diffuse dark spots and dorsal margin finely bordered by black. Pectoral, pelvic, and anal fins dusky. Caudal fin with 3 to 5 (most frequently 3) [5] irregular, wavy, dark bars formed by groups of chromatophores. Iris brownish orange, with diffuse dusky areas on dorsal and ventral portions.

FIGURE 51.—*Prochilodus mariae*, USNM 222839, 178.8 mm SL; Venezuela, Monagas, Río Orinoco, laguna Tapatapa.

DISTRIBUTION.—*Prochilodus mariae* is endemic to the Río Orinoco basin in Colombia and Venezuela and Río Casiquiare in Venezuela that drains into the upper Río Negro of the Río Amazonas basin (Figure 52, dots).

COMMON NAME.—Coporo de los Llanos (Venezuela).

BIOLOGY AND FISHERIES.—Flecker (1996:1845) demonstrated that the species is a functionally dominant species in the Andean foothill streams of the Río Orinoco basin. In his study, the experimental removal of all individuals of *Prochilodus mariae* from within artificial enclosures in that ecosystem resulted in dramatic shifts in both community structure and ecosystem attributes.

Prochilodus mariae is one of the most important species in the fisheries of the Río Orinoco basin. Novoa R. et al. (1982: 277) reported that *P. mariae* accounts for 15% of the total commercial fish landings at various localities in the Río Orinoco delta.

COMPARISONS.—As detailed in the "Diagnosis," *Prochilodus mariae* is readily distinguishable from its congeners by a combination of meristic characters and details of pigmentation.

REMARKS.—A prochilodontid specimen with 60 lateral-line scales that originated at Calabozo, Venezuela, in the central portions of the Río Orinoco basin was identified by Peters (1877:472) as *Prochilodus brama* (the *Semaprochilodus brama* of this study). This citation was repeated by Ulrey (1895:259) and Fowler (1950:216). Although *Semaprochilodus brama* has a high lateral-line scale count (56 to 68) that encompasses the value (60) in the specimen examined by Peters, that species is endemic to the Rio Xingú and Rio Tocantins basins in Brazil; those drainage systems are approximately 2000 km by water from the locality from which the specimen reported on by Peters originated. Mago-Leccia (1972:51) suggested that the specimen identified as *P. brama* by Peters (1877:472) was possibly *P. mariae* in light of the high number of lateral-line scales reported for that specimen. Our studies show that *P. mariae* possesses the highest number of lateral-line scales (52 to 64) within *Prochilodus*, a result that leads us to concur with Mago-Leccia's (1972) re-identification of the specimen reported on by Peters.

The citation by Fernández-Yépez (1969:55) of *Prochilodus asper* from the Río Caroni in the eastern portions of the Río Orinoco basin in Venezuela is a likely misidentification of *P. mariae* or *P. rubrotaeniatus*, given that *P. asper* is a junior synonym of *P. reticulatus*, a species endemic to the Lago Maracaibo basin of northwestern Venezuela and northeastern Colombia (see synonymy of *P. reticulatus*).

MATERIAL EXAMINED.—338 specimens (40, 29.6–366.5 mm SL).

COLOMBIA. *Meta:* Lago Mozambique, Hacienda Mocambique, ANSP 128143, 1 (1, 366.5); ANSP 128144, 1 (1, 341.0); ANSP 128786, 1 (1, 29.6); ANSP 135576, 4 (266.8–355.3) [1R]. Río Metica, approximately 3 km SE Hacienda Mozambique, ANSP 135557, 1 (1, 202.9); ANSP 135823, 1 (1, 231.0). Quebrada Venturoza, between La Balsa and Puerto López, ANSP 137763, 1 (1, 121.1). Lago Mozambique, Hacienda Humacita, ANSP 128784, 1 (1, 148.4). Río Negrito, bridge on road joining Puerto López to Villavicencio, ANSP 146861, 1 (131.5) [1R]. Garazoa, N of Villavicencio and Guaicaramo, USNM 100772. Río Meta, Barrigón (4°10'N, 73°01'W), CAS 15150, 1 (1, 234.0, holotype of *Prochilodus mariae*, formerly IU 15150, in part) [1R]; CAS 23942, 1 (1, 225.6, paratype of *Prochilodus mariae*, formerly IU 15150, in part) [1R]. Río Guaviare, FMNH 73418, 6 (1, 88.0–143.3) [1R]; USNM 181365, 4.

VENEZUELA. *Amazonas:* Río Orinoco, El Burro, ANSP 158863, 30 (2, 81.0–117.8); lots ANSP 158866 (2 specimens)

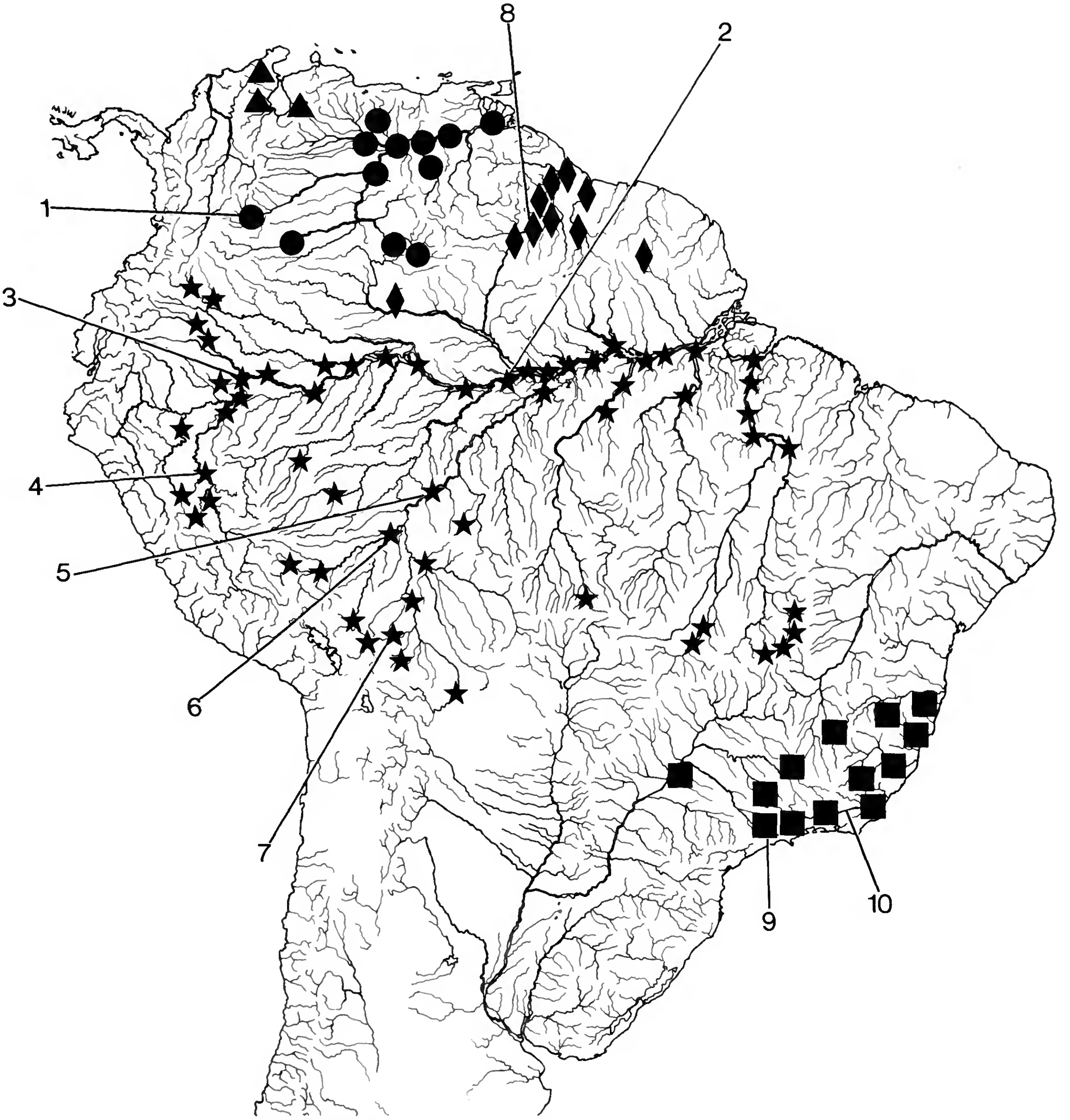


FIGURE 52.—Map of central and northern South America showing geographic distribution of *Prochilodus mariae* (dots; 1=holotype locality), *Prochilodus nigricans* (stars; 2=neotype locality of *Prochilodus nigricans;* 3=holotype locality of *Prochilodus ortonianus* and *Prochilodus cephalotes;* 4=holotype locality of *Prochilodus caudifasciatus;* 5=holotype locality of *Curimatus tigris;* 6=holotype locality of *Prochilodus beni;* 7=holotype locality of *Prochilodus labeo*), *Prochilodus reticulatus* (triangles, type locality inexact=lagune de Maracaïbo (Lago Maracaibo)), *Prochilodus rubrotaeniatus* (diamonds, type locality of *Prochilodus rubrotaeniatus* inexact =Rio Branco and Essequibo River; 8=holotype locality of *Prochilodus maripicru*), and *Prochilodus vimboides* (squares; 9=lectotype locality of *Prochilodus vimboides* and *Prochilodus oligolepis;* 10=Rio Paraíba do Sul, inexact type locality of *Prochilodus steindachneri;* see "Remarks" under *P. vimboides* concerning several questionable extralimital records for the species) (some symbols represent more than one collecting locality and/or lot of specimens).

and ANSP 158868 (7 specimens) intermingled =9 (1, 111.1–144.4). Caño Orera, close to El Burro, ANSP 158870, 4 (2, 89.4–113.8). Río Meta, approximately 20 minutes upriver of confluence with Río Orinoco, ANSP 158853, 29 (3, 98.4–286.6); ANSP 158854, 6 (244.6–305.8). Río Casiquiare, mouth of Río Curamuni, CAS-SU 56804, 2 (1, 107.9–108.6) [1R]. Río Mavaca, upstream of base camp, AMNH 93102, 2 (200.1–207.8). *Apure:* Río Apure, 10 km SW of San Fernando de Apure, CAS 34377, 3 (135.8–159.5). Río Apure, San Fernando de Apure, CAS-SU 56719, 9 (94.6–122.4). Río Apure, approximately 3 km W of fisheries station in San Fernando de Apure, MZUSP 27965, 12 (2, 88.5–116.9). Río Apure, Hacienda La Guanota near San Fernando de Apure, LIRP 1310, 8 (1, 35.3–79.4). Caño Cai-cara, at bridge on road from Montecal (7°22′N, 69°21′W), AMNH 77823, 26 (95.8–138.8). Río Apure (Las Guanotas), near San Fernando de Apure, USNM 256959, 10 (18.5–34.5; specimens cleared and counterstained for bone and cartilage). Río Apure, San Fernando de Apure, LIRP 1310, 8. *Bolivar:* Caño Caiman, where crossed by road between Caicara and Puerto Ayacucho, ANSP 158867, 4 (1, 119.6–145.3). Laguna La Teja, Caicara, CAS-SU 56716, 1 (152.2). Caño Quiribana, Caicara, CAS-SU 56806, 1 (115.3); CAS-SU 56809, 4 (119.0–134.2); CAS-SU 56811, 1 (131.3); CAS 58895, 2 (131.3–147.3). Small caño connected with Río Orinoco at El Burro, USNM 270243, 37 (3, 77.2–131.0). Small caño tributary to Río Mato, ANSP 13984, 1 (1, 154.5). Río Agua Blanca, near highway between Caicara and Ciudad Bolivar, ANSP 158857, 15 (1, 110.1–156.4). Río Urbana, on road between Maripa and Las Trincheras, ANSP 135780, 1 (145.3). Río Chaviripa, 15 km N of Manipure on road between Caicara and Puerto Ayacucho, ANSP 158856, 8 (1, 136.5–152.8). Río Orinoco, close to Puerto Las Majadas, ANSP 158865, 1 (140.5). *Delta Amacuro:* Mouth of caño Anabata, in front of Isla Portuguesa, ANSP 150097, 3 (1, 232.3–246.1). *Guárico:* Tributary of Río Guariquito, 24 km SSE on road to Cazorla, ANSP 130042, 4 (1, 103.0–109.8). Río Guariquito, MBUCV V-2499, 8. Río Orituco, 15 km SEE of Calabozo on road between Calabozo and Cazorla, ANSP 146530, 61 (1, 55.9–256.0). *Monagas:* Río Orinoco, laguna Tapatapa on Isla Tapatapa, USNM 222839, 2 (1, 123.7–178.8). Río Guarapiche, Caicara, USNM 163157, 1.

***Prochilodus nigricans* Agassiz, 1829**

FIGURES 52, 53; TABLE 14

Prochilodus nigricans Agassiz in Spix and Agassiz, 1829:64, pl. 39 [type locality: Brasiliae mediae fluviis (= rivers of central Brazil), restricted herein to Brazil, Amazonia; neotype designated herein; neotype locality: Brazil, Amazonas, Lago Janauacá].—Valenciennes in Cuvier and Valenciennes, 1850:80 [in part, Amazon, not cited specimen from Essequibo (River)].—Castelnau, 1855:63 [Río Tocantins].—Kner, 1859:148 [comparison with *Prochilodus binotatus*].—Günther, 1866:30 [Amazon]; 1868:229 [Peru, Xeberos].—Steindachner, 1874:532 [page 34 of reprint; comparison with *P. vimboides*]; 1881:132; 1883:12 [(Río) Huallaga].—Boulenger, 1898:5 [Ecuador, Río Santiago].—Eigenmann, 1910:424 [in part, not synonymy into *Prochilodus rubrotaeniatus*].—Pearson, 1924:29 [Bolivia, Tumupasa, Río Charquiti]; 1937a:90 [Peru, Paipay, Río Crisnejas].—LaMonte, 1935:7 [Brazil, Rios Purus and Jurua].—Fowler, 1940b:98 [Bolivia]; 1943:226 [Colombia, Florencia]; 1945:122 [in part, not cited occurrence of species in (Río de) La Plata basin]; 1950:221 [literature compilation, in part; not cited occurrence of species in eastern Brazil or Paraguay]; 1975:359 [literature compilation].—Eigenmann and Allen, 1942:46 [Peru, Amazon basin, not cited presence of species in (Río de) La Plata basin].—Géry, 1964:35 [Peruvian Amazon]; 1977:218 [Amazon basin].—Ringuelet et al., 1967:204 [in part, not cited occurrence of species in Paraguay or Ceará, Brazil].—Mago-Leccia, 1972:47 [use of caudal-fin pigmentation to distinguish species groups].—Saul, 1975: 112 [Ecuador, Napo (now Sucumbíos), Santa Cecilia; stomach contents].—Petrere, 1978:9 [importance of species in Amazonian fisheries]; 1985:7 [importance in Amazonian fisheries]; 1989:5 [importance in fish market at Manaus].—Goulding, 1980:244 [feeding habits].—Smith, 1981:21 [spawning period], 39 [migration in middle Rio Madeira].—Junk et al., 1983:406, table 3 [Brazil, Amazon; ecology].—Böhlke, 1984:148 [as possible senior synonym of *P. cephalotes*].—Lowe-McConnell, 1984:143 [economic importance]; 1987:128, table 6.1 [economic importance].—Nomura, 1984:54 [Brazil, common name].—Pauls and Bertollo, 1984:787 [karyotype].—Santos et al., 1984:27 [Brazil, Rio Tocantins; commercial importance; life history].—Araújo-Lima, 1985:430 [comparisons with other central Amazonian prochilodontids].—Lauzanne and Loubens, 1985:47 [Bolivia, Río Mamore].—Bertollo et al., 1986:156, table 1 [karyotype].—Carvalho and Merona, 1986:595 [lower Rio Tocantins; migration patterns].—Lauzanne et al., 1986:11.—Ortega and Vari, 1986:11 [Peruvian Amazon].—Géry et al., 1987:438 [not a component of Río Paraguay ichthyofauna].—Mérona, 1987:120 [Brazil, lower Rio Tocantins; ecology].—Mérona et al., 1987:81 [Brazil, Rio Tocantins; effects of impoundment on overall condition of population of species].—Stewart et al., 1987:23 [Ecuador, Río Napo].—Bayley, 1988:131, table 2 [growth rates].—Braga, 1990:549, table 1 [Brazil, Rio Tocantins; feeding and reproduction].—Lauzanne et al., 1991:67, table 1 [Bolivia, Amazon basin].—Mochek et al., 1991:115 [Peru, Ucayali; daily activity patterns].—Petrere et al., 1991:126 [growth rates].—Menezes and Vazzoler, 1992:63 [reproductive characteristics].—Mérona and Bitencourt, 1993:448 [Brazil, central Amazon; commercial fishery].—Mérona and Gascuel, 1993:99 [central Amazon flood plain; economic importance].—Roberts, 1993:68, fig. 6e,f [scale morphology].—Loubens and Panfili, 1995:17 [Bolivia, Río Mamoré basin; biology].—Chang, 1998:24, table 1 [southeastern Peru].—Ferreira et al., 1998:39, fig. 14 [Brazil, Amazonas, region of Santarém; commercial importance].—Mojica-C., 1999:554 [Colombia, Río Amazonas, Río Puto-mayo, Río Caquetá].—Santos and Ferreira, 1999:353 [Amazon basin].—Saint-Paul et al., 2000:239, 241 [Brazil, Amazonas, Lago do Inácio; relative abundance; occurrence in white waters].—Ortega et al., 2001:148 [Peru, Río Urubamba basin, Atalaya, Sepahua, Camisea].—Sánchez-Botero and Araújo-Lima, 2001:441 [Brazil, Manaus region; occurrence in aquatic macrophytes].—Silvano et al., 2001:126, fig. [Brazil, Amazonas, upper Rio Jurua].—Sivasundar et al., 2001:414 [limited genetic divergence in geographically widely separated populations].—Stewart et al., 2002:342 [Ecuador, Río Napo basin].—[Not Kner, 1959:146; Weyenberg, 1877:5; Bertoni, 1914:10; 1939:54; Pearson, 1937b:109; Fowler, 1941:168; 1950:221 [citation of species from Paraguay]; Eigenmann and Allen, 1942:57 [citation from (Río de) La Plata basin]; Pozzi, 1945:258; Ringuelet et al., 1975:72; Nomura, 1984:54; Lopez et al., 1987:19.]

Pacu nigricans.—Agassiz in Spix and Agassiz, 1829:64.—Müller and Troschel, 1844:84 [Brazil]; 1845:8, fig. 4. [Brazil].

Curimatus nigricans.—Valenciennes in Cuvier and Valenciennes, 1850:90 [cited as synonym of *Prochilodus nigricans* Agassiz, 1829].

Prochilodus ortonianus Cope, 1878:685 [type locality: Nauta, Peru (= Peru, Loreto, Nauta, confluence of Ríos Marañon and Ucayali)].—Eigenmann and Eigenmann, 1891:48 [in listing of South American fishes].—Fowler, 1906: 311 [redescription based upon holotype]; 1911:497 [comparison with *Prochilodus stigmaturus*]; 1940a:258 [Peru, Río Ucayali basin, Boca Chica]; 1945:121 [Peru, Nauta and Boca Chica]; 1950:222 [literature compilation]; 1975:359 [literature compilation.—Pellegrin, 1909a:148 [Brazil, Manaos (= Manaus), Rio Negro, Teffé, Tonantins, Tabatinga].—Eigenmann, 1910:424

[in listing of South American fishes].—Eigenmann and Allen, 1942:46 [Peru, lower Río Marañon basin].—Mago-Leccia, 1972:47 [use of caudal-fin pigmentation to distinguish species groups].—Géry, 1977:218 [Amazon basin].—Böhlke, 1984:148 [holotype depository].—Ortega and Vari, 1986:11 [Peruvian Amazon].

Prochilodus cephalotes Cope, 1878:686 [type locality: Peruvian Amazon, restricted by Fowler (1950:217) to Nauta, Amazonas peruano (= Peru, Loreto, Nauta, confluence of Rios Marañon and Ucayali)].—Eigenmann and Eigenmann, 1891:48 [in listing of South American fishes].—Fowler, 1906:312 [redescription based upon holotype]; 1911:497 [comparison with *Prochilodus stigmaturus*]; 1940a:287 [Peru, Río Ucayali basin]; 1945:121 [Peru]; 1950: 217 [literature compilation]; 1975:358 [literature compilation].—Eigenmann, 1907b:768 [lateral-line scale count]; 1910:424 [in listing of South American fishes].—Eigenmann and Ogle, 1907:5 [cited similarity to *P. beani*].—Steindachner, 1907:152 [similarity to *P. lacustris*].—Pellegrin, 1909a:148 [Brazil, Tabatinga].—Eigenmann and Allen, 1942:46 [Peru, lower Río Marañon basin].—Géry, 1972b:33 [comparison with *Curimatus* (=*Prochilodus*) *tigris*]; 1977:218 [*P. cephalotes* as possibly based upon juvenile of *P. nigricans*].—Mago-Leccia, 1972:47 [use of caudal-fin pigmentation to distinguish species groups].—Böhlke, 1984:148 [holotype depository].—Ortega and Vari, 1986:11 [Peruvian Amazon].

Prochilodus rubrotaeniatus [not of Jardine, 1841].—Eigenmann and Eigenmann, 1891:48 [Peruvian Amazon].—Eigenmann and Allen, 1942:46 [in listing of South American fishes; in part, specimens from upper Amazon].—Géry, 1964a:40 [Peruvian Amazon]; 1977:218 [in part, specimens from upper Amazon].—Ortega and Vari, 1986:11 [Peru, Amazon basin].—Stewart et al., 1987:23 [Ecuador, Río Napo].—Not Eigenmann and Allen, 1942:46.

Prochilodus reticulatus [not of Valenciennes].—Perugia, 1897:25 [Bolivia, upper Río Beni].—Eigenmann, 1910:424 [in part, Bolivia, Alto Beni (= upper Río Beni)].—Pearson, 1937b:109 [(Río) Beni-Mamoré basin].—Fowler, 1940b:98 [Bolivia]; 1950:222 [literature compilation, in part; citation of species from Amazon].

Prochilodus caudifasciatus Starks, 1906:773, fig. 5 [type locality: Río Perené at Perené (Huánuco), Peru].—Fowler, 1940a:287 [Peru, Río Ucayali basin]; 1945:122 [Peru]; 1950:217 [literature compilation]; 1975:358 [literature compilation].—Mago-Leccia, 1972:47 [use of caudal-fin pigmentation to distinguish species groups].—Géry, 1977:219 [Peru].—Lauzanne et al., 1986:11 [Bolivia, Trinidad, Yucumo, Madre de Dios, Río Itenez].—Ortega and Vari, 1986:11 [Peruvian Amazon, common name].—Vari and Howe, 1991:34 [holotype depository].

Prochilodus caudofasciatus.—Eigenmann, 1910:424 [unjustified emendation of species name].—Eigenmann and Allen, 1942:48 [Peru, lower Río Ucayali basin].

Curimatus tigris Fowler, 1914:518, fig. 2 [type locality: tributaries of the Madeira River near Porto Velho, Brazil (= Brazil, Rondônia, Porto Velho, tributaries of Rio Madeira)].—Myers, 1929:621 [cited as possible *Prochilodus* species].—Géry, 1965:35; 1972b:33 [cited as probable synonym of *Prochilodus cephalotes*].—Böhlke, 1984:67, 148 [depository of holotype and paratypes; confirmed as member of Prochilodontidae].—Géry et al., 1987: 438 [comparisons with juvenile of *Prochilodus lineatus*].—Vari and Howe, 1991:19 [paratype depository].

Prochilodus migricans.—Starks, 1913:15 [species name misspelled; Brazil, Pará and Rio Madeira].

Prochilodus beni Pearson, 1924:29, pl. 9: fig. 2 [type locality: Bolívia, Río Beni basin, Cachuela Esperanza]; 1937b:109 [Beni-Mamoré basin].—Fowler, 1940b:98 [Bolivia]; 1950:215 [literature compilation]; 1975:358 [literature compilation].—Mago-Leccia, 1972:47 [use of caudal pigmentation patterns to discriminate species groups].—Géry, 1977:218 [Bolivia].

Prochilodus humeralis [not of Günther, 1859].—Ridoutt, 1939:69 [misidentification; included figure apparently based upon Eigenmann, 1922a, pl. 20].—Ringuelet, 1975:94 [citation apparently based upon Ridoutt, 1939].—[Not Fowler, 1945:124.]

Pacus nigricans.—Fowler, 1941:168 [in synonymy of *Prochilodus nigricans* Agassiz, 1829, generic name misspelled].

Curimata tigris.—Fowler, 1950:293, fig. 353 [literature compilation].

Ichthyoelephas maripicru [not of Eigenmann, 1912].—Ovchynnyk, 1971:105 [Ecuador, Napo, Río Jivino].

Prochilodus tigris.—Fowler, 1975:360 [literature compilation].

Prochilodus corimbata.—Lowe-McConnell, 1975:74 [importance in fish market at Manaus, Brazil; common name].

Ichthyoelephas humeralis [not of Günther, 1859].—Ortega and Vari, 1986:11 [Peruvian Amazon; based upon Ridoutt, 1939].

Prochilodus labeo Loubens et al., 1991:231 [type locality: Bolivia, Villa Tunari, Río Chaparé, bassin de Mamore (= Bolivia, Villa Tunari, Río Chaparé, Río Mamoré basin].

DIAGNOSIS.—The dark, irregular, wavy, bar-like patterns on the caudal-fin lobes in *Prochilodus nigricans* discriminate that species from *P. argenteus, P. britskii, P. costatus, P. hartii, P. lineatus, P. magdalenae, P. reticulatus*, and *P. vimboides*, which lack such caudal-fin pigmentation. Within the group of *Prochilodus* species with dark, irregular caudal-fin bars, *P. nigricans* differs from *P. mariae* in the number of scales along the lateral line (44 to 51, 48 most frequent, versus 52 to 64, 52 in only 2.5% of specimens examined for this feature, respectively); from *P. brevis* in the form of the scales (with complex pattern of variable subdivisions versus having only radial subdivisions), the modal number of scales along the lateral line (44 to 51 with 47 to 51 scales in 95.9% of the 170 specimens from which this count was taken, versus 41 to 48, 43 most frequent and 47 or 48 scales in only 3.25% of the specimens examined for this feature, respectively), and the pronounced modal differences in the number of vertebrae (40 to 45, 43 and 44 most frequent and 40 in only 2.0% of specimens examined for this feature, versus 40 to 42, 40 most frequent and 42 in only 7.1% specimens examined for this feature, respectively); from *P. lacustris* in the form of the scales (with complex pattern of variable subdivisions versus having only radial subdivisions), the number of horizontal rows of scales between the pelvic-fin insertion and the lateral line (7 to 9, 8 most frequent and 9 in only 11.8% of specimens examined for this feature, versus 8 to 11, 9 most frequent and 8 present in only 15.7% of specimens examined for this feature, respectively); from *P. rubrotaeniatus* in the number of horizontal rows of scales around the caudal peduncle (17 to 21 with 19 most frequent and 17 in only 2 of 208 specimens, versus 14 to 18 with 16 most frequent and 17 in only 10.8% of specimens, respectively; Figure 54), the number of horizontal rows of scales between the pelvic-fin insertion and the lateral line (7 to 9, 8 most frequent, versus 6 or 7, 6 most frequent, respectively; Figure 55), and the range and mode of lateral-line scales (44 to 51, 49 most frequent and 44 to 46 in only 3% of specimens, versus 44 to 48 with 45 most frequent and 47 and 48 in only 10% of specimens, respectively; Figure 56).

DESCRIPTION.—Morphometric and meristic data for *Prochilodus nigricans* presented in Table 14. Body comparatively high, transversely compressed. Greatest body depth at dorsal-fin origin. Dorsal profile of head gently concave to straight. Predorsal profile of body convex. Body profile posteroventrally inclined along dorsal-fin base; straight from posterior of dorsal-fin base to adipose-fin origin, and concave along

TABLE 14.—Morphometrics and meristics of *Prochilodus nigricans:* (A) neotype of *Prochilodus nigricans,* MZUSP 21574; (B) holotype of *Curimatus tigris,* ANSP 39156; (C) holotype of *Prochilodus beni,* CAS 58881; (D) holotype of *Prochilodus caudifasciatus,* USNM 53473; (E) holotype of *Prochilodus cephalotes,* ANSP 21211; (F) holotype of *Prochilodus labeo,* MNHN 1989-120; (G) holotype of *Prochilodus ortonianus,* ANSP 21267; and (H) all specimens of *Prochilodus nigricans* from which counts and measurements were taken. Standard length is presented in mm; values 2 to 16 are percentages of SL, 17 to 21 are percentages of HL. Dash indicates unobtainable datum as a consequence of condition of specimens, and question mark indicates specimen damaged for the indicated feature.

Characters	A	B	C	D	E	F	G	H
				Morphometrics				
1. Standard length	364.2	20.7	47.1	246.1	55.1	253.5	165.9	31.2–365.7
2. Greatest body depth	34.5	35.7	41.2	30.1	35.6	33.4	33.5	28.4–42.9
3. Predorsal length	44.3	51.2	49.7	47.2	49.2	45.0	45.6	42.9–51.2
4. Dorsal-fin base length	16.7	15.5	17.8	18.0	17.4	17.4	17.8	14.4–19.5
5. Dorsal fin to adipose fin distance	27.2	27.1	24.2	29.3	27.4	26.8	28.3	22.3–30.6
6. Dorsal to caudal fin distance	44.1	44.4	38.4	45.4	42.3	44.5	44.0	37.9–47.2
7. Prepelvic length	49.9	56.5	55.8	51.7	54.3	49.9	50.9	46.4–57.6
8. Preanal distance	77.4	79.2	79.6	78.1	78.6	76.6	79.0	72.3–83.1
9. Snout to anal-fin insertion	79.6	80.2	81.5	82.2	81.3	78.9	82.6	75.1–89.2
10. Anal-fin base length	12.1	11.1	10.9	11.1	10.7	9.5	11.5	8.9–13.2
11. Caudal-peduncle length	13.1	14.0	12.1	14.3	12.9	14.9	12.8	10.6–15.9
12. Dorsal-fin length	25.0	36.7	38.4	30.2	–	28.9	26.0	24.0–39.9
13. Pectoral-fin length	20.5	–	19.7	22.6	–	20.9	21.8	18.7–24.6
14. Pelvic-fin length	21.3	19.3	20.8	22.1	–	20.4	20.7	16.8–24.3
15. Least caudal-peduncle height	11.3	12.1	12.1	12.6	10.5	12.1	11.8	10.2–13.8
16. Head length	25.8	36.7	34.2	28.9	36.5	27.0	29.8	24.0–36.7
17. Snout length	42.9	25.0	34.8	48.6	35.3	45.3	39.6	25.0–56.4
18. Bony orbital diameter	17.7	25.0	31.1	15.8	25.9	19.0	24.4	15.3–39.7
19. Postorbital length	43.9	46.1	39.1	37.6	39.8	40.1	41.4	33.3–46.1
20. Interorbital width	57.9	47.4	50.9	53.7	49.8	55.1	52.7	47.4–64.9
21. Mouth width	46.1	31.6	44.1	45.2	38.3	46.1	45.1	31.6–59.1
				Meristics				
Lateral-line scales	49	43?	49	47	45?	48	49	44–51
Scale rows between dorsal-fin origin and lateral line	10	9?	11	8	10?	10	10	7–11
Scale rows between anal-fin origin and lateral line	6	7	8	6	7?	7	7	6–8
Scale rows between pelvic-fin insertion and lateral line	8	8	9	7	8?	9	8	7–9
Rows of scales around caudal peduncle	18	20?	20	18	18	18	18	17–21
Median predorsal scales	17	15	18	16	15	16	16	13–20
Median scales between dorsal and adipose fins	15	17	18	17	15	17	18	14–20
Vertebrae	44	44	45	42	44	43	44	40–45
Inner row teeth, upper jaw	24	15?	19	25	20	26	18	14–29
Inner row teeth, lower jaw	12	12	12	15	12	15	12	8–18

caudal peduncle. Predorsal portion of body with moderate median ridge. Postdorsal portion of body obtusely rounded transversely. Ventral profile of body convex from tip of lower jaw to posterior of anal-fin base. Ventral profile of caudal peduncle concave. Prepelvic region transversely flattened proximate to pelvic-fin insertion. Moderately developed median keel present between pelvic-fin insertion and anus.

Head profile pointed. Mouth terminal. Snout length greater than horizontal width of orbit. Nares of each side of head close to each other; anterior nares circular, posterior nares crescent shaped. Adipose eyelid present but poorly developed; most developed anteriorly, but with greater part of eye uncovered. Lips fleshy, moderately developed relative to condition in some prochilodontids, and forming oral disk when protracted.

Functional teeth in two rows in each jaw. All teeth movably implanted in flesh that overlies jaws. All teeth of similar size, with exposed portions spoon shaped except when worn down. Inner tooth series in each jaw with 14 to 29 teeth on left side of upper jaw and 8 to 18 teeth on left side of lower jaw. Outer row of teeth in each jaw with approximately 111 teeth on each side of upper jaw and 76 teeth on each side of lower jaw in neotype. Upper and lower lips bordered by numerous globular, fleshy papillae.

Scales spinoid. Scales in middorsal series between posterior of dorsal fin and adipose-fin origin similar in form to those of adjoining regions of body. Lateral line with 44 to 51 (35.4% of specimens with 49) pored scales; 7 to 11 (47.8% of specimens with 9) horizontal rows of scales between dorsal-fin origin and lateral line; 7 to 9 (51.1% of specimens with 8) horizontal rows of scales between pelvic-fin insertion and lateral line; 6 to 8

FIGURE 53.—*Prochilodus nigricans*, neotype, MZUSP 21575, 364.2 mm SL; Brazil, Amazonas, Lago Janauacá, right margin of Rio Solimões.

(56.9% of specimens with 7) horizontal rows of scales between anal-fin origin and lateral line; 13 to 20 (34.9% of specimens with 17) median predorsal scales; 14 to 20 (37.6% of specimens with 16) scales in middorsal series between posterior of dorsal-fin base and adipose-fin origin; 17 to 21 (49.8% of specimens with 19) horizontal rows of scales around caudal peduncle.

Dorsal fin preceded by small, but well-developed, anteroventrally bifurcate, procumbent spine somewhat triangular in lateral view. Dorsal-fin rays (including procumbent spine) iii,9 to 11 (iii,10 most frequent) [iii,10]; anal-fin rays iii,7 to 9, or ii,8 or 9 (iii,8 most frequent) [iii,8]; pectoral-fin rays i,13 to 17 (i,15 most frequent) [i,15]; pelvic-fin rays i,8 or 9 (i,8 most frequent) [i,8]; principal caudal-fin rays 10/9 [10/9].

Vertebrae 40 to 45 (36.0% of specimens with 43).

Dorsal fin truncate, slightly pointed distally; posterior unbranched and anterior branched rays longest and subequal. Dorsal-fin origin located closer to tip of snout than to caudal-fin base. Greatest length of adipose fin approximately equal to horizontal width of orbit, its origin located along vertical that passes through posterior one-third of anal-fin base. Pectoral fin distally pointed. Tip of adpressed pectoral fin extending posteriorly to, or nearly to, pelvic-fin insertion. Pelvic fin falcate. Pelvic-fin insertion located along vertical that passes approximately through middle of dorsal-fin base. Tip of adpressed pelvic fin reaching approximately two-thirds to four-fifths of distance from pelvic-fin insertion to anus. Axillary scale present, its length approximately one-third of greatest length of pelvic fin. Posterior unbranched and anterior branched anal-fin rays longest and subequal. Caudal fin moderately bifurcate.

COLORATION IN ALCOHOL.—Ground coloration silvery yellow or brownish yellow, with dorsal portion of body and head darker. Lateral portion of body with 4 to 18 vertically elongate, dark, diffuse, irregular patches between head and caudal fin. Patches with approximate overall form of narrow isosceles triangles, with apex positioned on middle of ventrolateral portion of body and base on dorsomedial region of body. Patches well developed in small specimens, but indistinct or absent in large individuals. Lateral surface of body with approximately 6 to 14 [7] dark, wavy, horizontal stripes along dorsal and ventral margins of exposed portions of scales. Approximately 3 to 6 (most frequently 6) [4] wavy stripes dorsal to, and 2 to 8 (most frequently 5) [3] wavy stripes ventral to, lateral line; number of stripes lower in large specimens, such as the neotype. Field of black or brown chromatophores forming dark mark of irregular shape on upper one-half of opercle.

Dorsal fin with 4 to 10 (most frequently 5) [5] dark, irregular stripes beginning along anterior margin and extending across fin approximately parallel to base of fin. Adipose fin with small, dark spots and with dorsal margin finely bordered with black. Pectoral, pelvic, and anal fins dusky. Caudal fin with 2 to 8 (most frequently 4) [6] irregular, wavy, dark, vertical bar-like patterns formed by spots of dark chromatophores. Iris yellowish golden or brownish yellow, with diffuse dusky areas on dorsal and ventral regions. Some specimens, typically those that originated in acidic black waters, with overall pigmentation much darker than typical for species.

COLORATION IN LIFE.—(Based upon a color transparency of recently collected adults from the Río Ucayali basin, Ucayali, Peru, taken by the second author). Dark pigmentation as described above. Ground coloration silvery, dorsal portion of body and particularly head distinctly darker. Pectoral and particularly pelvic fins yellowish orange. Other fins hyaline.

DISTRIBUTION.—*Prochilodus nigricans* is widely distributed along the main stream and western and southern tributaries of much of the Rio Amazonas and through the Rio Tocantins basin. This species is apparently absent in the Rio Negro and Rio

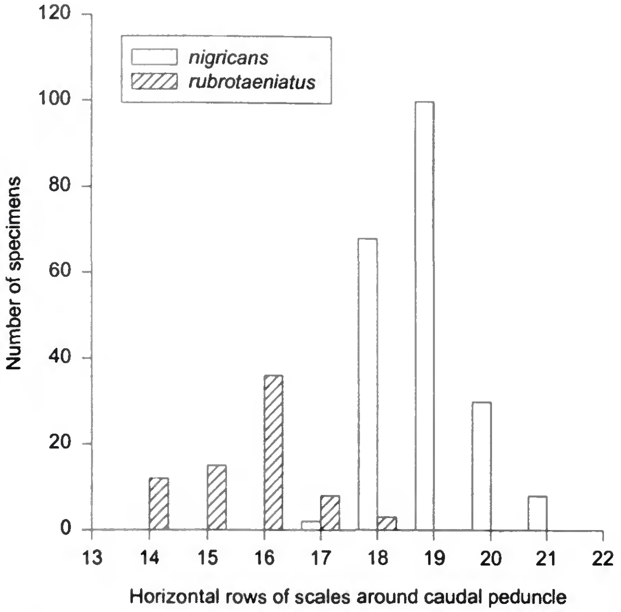


FIGURE 54.—Histogram of number of horizontal rows of scales around caudal peduncle plotted against number of specimens with particular counts in *Prochilodus nigricans* and *Prochilodus rubrotaeniatus*.

Branco basins and other northern tributaries to the Rio Amazonas (Figure 52, stars).

COMMON NAME.—Grumatã, curimatá, corimatá (Brazil), Boquichico (Peru).

COMPARISONS.—The combination of the presence of a pattern of dark caudal-fin pigmentation and various meristic features unambiguously distinguishes *Prochilodus nigricans* from all of its congeners with the exception of three species: *P. brevis, P. lacustris,* and *P. rubrotaeniatus*. *Prochilodus nigricans* of the Rio Amazonas and Rio Tocantins basins has a distribution distinctly separated from that of *P. brevis,* which is endemic to the eastern and northeastern portions of Brazil (Figures 30, 52). The two species differ in the form of the scales (with complex pattern of variable subdivisions in *P. nigricans* versus having only radial subdivisions in *P. brevis*), and in the modal values for the number of scales along the lateral line. Although there is some overlap in the ranges for number of lateral-line scales, much of the overlap represents a small percentage of the specimens of each species (see "Diagnosis"). *Prochilodus nigricans* is consequently considered to be distinct from *P. brevis*.

Prochilodus nigricans differs from *P. lacustris* of northeastern Brazil in the form of the scales (with complex pattern of variable subdivisions versus having only radial subdivisions) and less trenchantly in the modal values and ranges in the number of horizontal rows of scales between the pelvic-fin insertion and the lateral line and in the number of median predorsal scales. The two species are consequently recognized as separate herein.

Prochilodus nigricans, which is widely distributed through the white-water systems of the western and southern portions of the Rio Amazonas and Rio Tocantins systems, and *P. rubrotaeniatus,* of the black- and clear-water drainage systems of the Guianas and the northern portions of the Rio Negro basin, differ from each other both in the range and mode of the number of horizontal rows of scales around the caudal peduncle (17 to 21 in *P. nigricans* with modal value of 19, versus 14 to 18 in *P. rubrotaeniatus* with modal value of 16; Figure 54) and to a lesser degree in the number of horizontal rows of scales between the pelvic-fin insertion and the lateral line (see "Diagnosis" and Figure 55). Because of these differences and the ecological and geographic separation of these species, the two species are recognized as distinct in this study.

REMARKS.—Agassiz's (in Spix and Agassiz, 1829:64, pl. 39) description of *Prochilodus nigricans* was based upon a specimen of approximately 185.0 mm SL that had been collected by Spix and Martius, presumably in some portion of the Brazilian Amazon (see Papavero, 1971, map 7, for itinerary of that collecting expedition). According to Kottelat (1988:69), "the specimens collected by Spix (except those subsequently given to Agassiz) were housed in Zoologische Staatssammlung München until their destruction during a British bombing raid on the night of 24–25 April, 1944." Furthermore, the holotype of *Prochilodus nigricans* was not listed by Kottelat (1988:84) as being deposited in the collections of museums known to hold types of species collected by Spix, nor were any types cited by Eschmeyer et al. (in Eschmeyer, 1998:1178). We con-

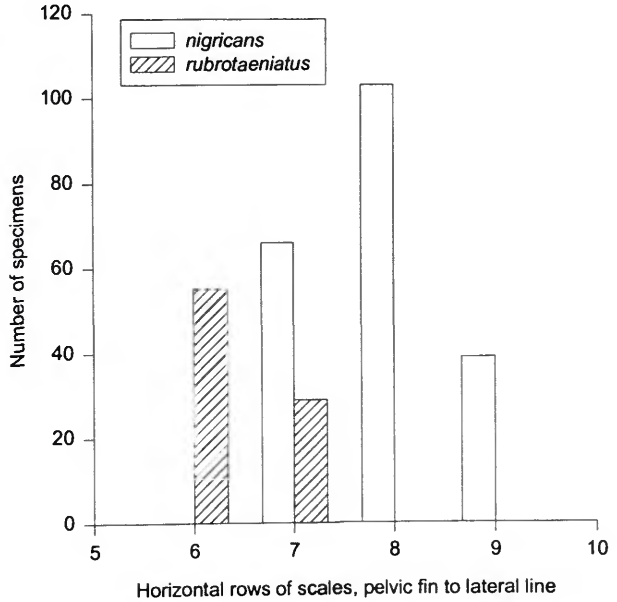


FIGURE 55.—Histogram of number of horizontal rows of scales between pelvic-fin insertion and lateral line plotted against number of specimens with particular counts in *Prochilodus nigricans* and *Prochilodus rubrotaeniatus*.

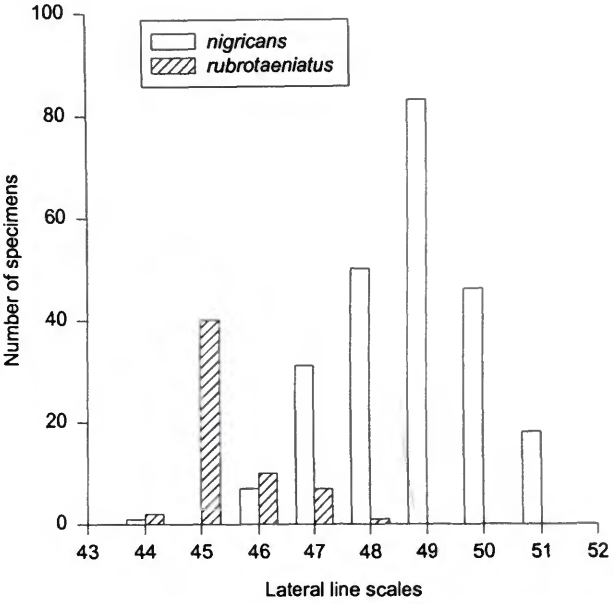


FIGURE 56.—Histogram of number of lateral-line scales plotted against number of specimens with particular counts in *Prochilodus nigricans* and *Prochilodus rubrotaeniatus*.

sequently presume that the holotype of *Prochilodus nigricans* is no longer extant.

The original description of *Prochilodus nigricans* and the accompanying illustration (Agassiz in Spix and Agassiz, 1829) matches the only *Prochilodus* species in the Amazon basin with dark caudal-fin markings, which is identified herein as *P. nigricans*. Nonetheless, there has been great confusion as to the identity of *P. nigricans* as is amply demonstrated by the complex synonymy for that species and in the reports of *P. nigricans* from areas far beyond its actual geographic range. In light of the similarity of *Prochilodus nigricans* and some of its congeners, most notably *P. rubrotaeniatus,* and in order to stabilize the nomenclature of the species, we herein designate as the neotype for *Prochilodus nigricans* a 364.2 mm SL specimen (MZUSP 21575) that originated at Lago Janauacá along the Rio Solimões in the central portions of the Amazon basin, a region in which Spix and Martius collected (see Papavero, 1971:66–67 and map 7 for the itinerary of that collecting expedition).

A series of authors subsequent to Agassiz (in Spix and Agassiz, 1829) described a number of what are herein considered to be junior synonyms of *Prochilodus nigricans*. This subsequent confusion is, to a degree, a consequence of the intraspecific geographic and ecophenotypic variation present in the species that can be difficult to recognize in the absence of population samples from across the broad distributional range of the species. Such samples were typically unavailable to many of the authors who published on prochilodontids subsequent to Spix.

Cope (1878:685–686) described two nominal species, *Prochilodus ortonianus* and *P. cephalotes,* from material that originated in the Peruvian Amazon. No differences were found in the meristic and morphometric features and other characters examined in this study that would distinguish either of those two nominal forms from *P. nigricans* (Table 14). Both *P. ortonianus* and *P. cephalotes* are consequently considered to be junior synonyms of *P. nigricans.*

The description of *Prochilodus caudifasciatus* by Starks (1906:773–774, fig. 5) was based upon an evidently malnourished specimen of *P. nigricans* from the Río Perené, Peru, an Andean piedmont river system (see also comments below concerning *P. labeo*). Consequences of that condition include the proportionally more elongate overall form of the head and the more prominent lips than are typical in well-feed individuals of *P. nigricans.* The malnutrition demonstrated by the holotype of *P. caudifasciatus* may represent either a seasonal reduction in available detritus and/or periphyton in the region from which the specimen originated or may reflect the limited amounts of organic particulate matter present throughout the yearly cycle in more rapidly flowing Andean piedmont water bodies, such as the type locality. No other differences were found to discriminate *P. caudifasciatus* from *P. nigricans* during this study (Table 14), and *P. caudifasciatus* is consequently considered to be a junior synonym of *P. nigricans.* It is likely that literature citations of *P. caudifasciatus* by subsequent authors were based either upon similarly poorly nourished specimens of *P. nigricans* or upon specimens that had been collected from sites in close geographic proximity to the type locality of *P. caudifasciatus.*

The description of *Curimatus tigris* (Fowler, 1914:518–520, fig. 2) was based upon a series of small specimens (holotype 20.7 mm SL; paratypes 10.6–22.3 mm SL) that originated in the Rio Madeira, Brazil. Myers (1929:62) proposed that these specimens were actually juveniles of a *Prochilodus* species. Available evidence indicates that this nominal species cannot be distinguished from juveniles of *P. nigricans*. *Curimatus tigris* is consequently considered to be a junior synonym of (see Table 14).

Pearson's description of *Prochilodus beni* (1924:29, pl. 9: fig. 2) was based upon a juvenile prochilodontid collected in the Río Beni basin, Bolivia, which is apparently *P. nigricans* (see Table 14). *Prochilodus nigricans* is the only prochilodontid known from the Río Beni system. *Prochilodus beni* is placed herein into the synonymy of *P. nigricans.*

Most recently Loubens et al. (1991) described *Prochilodus labeo* from the uplands of Bolivia, a habitat peripheral to the detritus rich lower elevation water bodies where members of the family are most common. Those authors proposed their species on the basis of the greater development of the lips, the proportionally smaller orbit, and details of body form. *Prochilodus argenteus* (see von Ihering and Azevedo, 1934, pl. 4) and *P. lineatus* (see Angelescu and Gneri, 1949) assume such body forms when malnourished, with various proportional measurements undergoing consequent notable shifts. The broad range of body forms in *P. lineatus* from different habitats was more recently discussed by Sverlij et al. (1993:3), who noted that Cabrera and Candida (1964), Vidal (1967), and Pignalberi and Cordiviola de Yuan (1973) found that there often are distinctly different body forms within populations of that species, evidently as a consequence of both biotic and abiotic factors. Observations by the first author on specimens of *P. lineatus* from the upper Rio Paraná basin in aquarium settings have shown that one response to decreased availability of detritus is an increase in the proportional size of the lips. Differences in relative lip size also were noted during underwater observations of *P. lineatus* by the authors in different habitats in the Rio Miranda basin, Mato Grosso do Sul, Brazil. In that region, individuals living over sand bottoms had thicker lips but more attenuate bodies than did specimens in populations from the adjoining main river channel. Such enlarged lips, in turn, results in a proportional decrease in the relative orbit size. Thus, the proportional differences that involve the snout and the relative width of the orbit apparently are a function of ecophenotypic and diet-induced variation, and we judge them to be of questionable utility in discriminating species.

In their description of *Prochilodus labeo*, Loubens et al. (1991, fig. 9) recognized three forms of the genus from various localities in Bolivia. The first of these was *P. nigricans*, a broadly distributed species (see "Distribution"), the second a form that they identified as *P.* cf *nigricans*, and the third their new species, *P. labeo*. The specimens of *P. labeo*, including the paratypes, came from two localities, and this material formed two discrete clusters in the principal components analysis. Several points are of note relative to the question of the recognition of *P. labeo*. The degree of difference between the two samples of that species in the analysis are as great as, or greater than, those between some individuals of *P. labeo* and what those authors recognized as *P. nigricans*. The degree of difference also is distinctly greater than the separation in the plot between some individuals of *P. labeo* and many specimens of *P.* cf. *nigricans*, which in the analysis lies between and significantly overlaps with *P. nigricans*. It also is striking that the arrangement of the samples of the three nominal forms (*P. nigricans* to *P.* cf. *nigricans* to *P. labeo*) correlates with the increasing elevation of the collecting sites from which the samples originated. As noted by Loubens et al. (1991:234), "*P. labeo* sp. n. appears to complete the series of fishes with large lips and long snouts that in the Prochilodidae [=Prochilodontidae] were formed in the waters of South America mountains." Our analysis has found that other such upland nominal species are evidently ecophenotypic variants of the more typical morphotypes of species that occur in the more nutrient-rich lowlands of the Neotropics. Examination of a broader sample of *P. nigricans* than were available to Loubens et al. (1991) indicates that *P. labeo* falls within the range of variation for *P. nigricans* within the type region of *P. labeo*, and the latter species is consequently placed herein in the synonymy of *P. nigricans*.

Ridoutt (1939:69) cited *Prochilodus* (=*Ichthyoelephas*) *humeralis* for the Ríos Urubamba and Perené, southeastern Peru. He, however, neither discussed the basis for this identification nor cited voucher specimens for that record. All subsequent citations of this species from the Amazon basin are apparently based upon Ridoutt (1939). *Ichthyoelephas humeralis* is endemic to the coastal rivers of the Pacific versant of Ecuador, and the Ridoutt citation of that species from Cis-Andean Peru is consequently erroneous. In light of the fact that *Prochilodus nigricans* is the only member of the Prochilodontidae that this study and Ortega et al. (2001:148) found to be present in the region from which Ridoutt reported *Ichthyoelephas humeralis*, we consider all citations of *I. humeralis* from the Peruvian Amazon to refer to *P. nigricans*.

Prochilodus rubrotaeniatus has been cited by various authors as occurring in portions of the Amazon basin outside of the Rio Branco and Rio Marauiá of Brazil, the only regions within the Amazon drainage from which we have examined material of the species. These records, all of which lie outside the known range of *P. rubrotaeniatus* as defined herein, are considered to represent misidentifications of the morphologically similar *P. nigricans*.

Ovchynnyk (1971:105–106, fig. 11, table 11) identified a specimen that originated in the Río Jivino in the Amazonian basin of Ecuador as *Ichthyoelephas maripicru* without commenting on the basis for his shift of the species from *Prochilodus* to *Ichthyoelephas*. *Prochilodus maripicru* is herein recognized as a junior synonym of *P. rubrotaeniatus*, a species not known from the Ecuadorian Amazon. That record of *Ichthyoelephas maripicru* from eastern Ecuador is considered to be a misidentification of *P. nigricans*.

Various citations of *P. argenteus* and *P. reticulatus* (see synonymy) from Amazonian localities are considered erroneous within the context of the results of this study under which *P. argenteus* is considered to be endemic to the Rio São Francisco system of eastern Brazil, and *P. reticulatus* is considered to be limited to the rivers of the Lago Maracaibo basin, northwestern Venezuela. These records are treated herein as misidentifications of *P. nigricans*.

MATERIAL EXAMINED.—915 specimens (140, 31.2–365.7 mm SL; partial meristic data taken from additional 136 specimens).

NEOTYPE.—BRAZIL. *Amazonas:* Lago Janauacá, right margin of Rio Solimões (3°28′S, 60°17′W), collected by Alpha Helix Expedition, 7–25 Jan, 1977, MZUSP 21575, 1 (1, 364.2; designated herein).

BOLIVIA. *Beni:* Coitarama, MNHN uncatalogued, 1 (1, 304.7) [1R]. Cachuela Esperanza (first rapids of river), Río Beni, CAS 58881 (formerly IU 17288), 1 (1, 47.1, holotype of *Prochilodus beni*) [1R]. Provincia Ballivia, Río Curiraba, approximately 10 km NE of Estação Biológica de El Parvenir; approximately 40 air km E of San Borgia, USNM 320632, 2 (1, 187.5–284.4). Provincia Ballivia, Río Matos, at crossing with road, 48 km E of San Borja (approximately 14°56′S, 66°17′W), USNM 317363, 3 (1, 263.7–331.0). Estacion Biologica de Beni "campamento trapiche," 500 m upriver of bridge on Río Curiraba, USNM 301899, 1 (1, 157.4) [1R]. 300 m from Estacion Biologica de Beni, "campamento trapiche," Río Curiraba, USNM 301903, 1 (1, 152.8) [1R]. Río Mamoré, approximately 13°35′S, AMNH 77405, 13 (92.1–194.1). Río Iténez, 10 km SE of Costa Marques, Brazil (approximately 12°28′S, 64°16′W), AMNH 39810, 1 (1, 125.9) [1R]; UMMZ 205227, 1 (1, 131.2) [1R]. Laguna Motocusal, near Río Isiboro (approximately 15°28′S, 65°05′W), USNM 278569, 2. *Cochabamba:* Confluence of Ríos Chaparé and Coni (approximately 15°58′S, 64°42′W), MNHN uncatalogued, 1 (1, 363.4) [1R]; Río Mamoré basin, Río Chaparé, Villa Tunari, MNHN 1989-120, 1 (1, 253.5; holotype of *Prochilodus labeo*). *La Paz:* Tumupasa, CAS 59303 (formerly IU 17286), 9 (1, 135.5–168.2) [1R]; USNM 86844 (formerly IU 17286), 5 (3, 126.2–138.3); USNM 231438, 1 (cleared and stained). Río Charquiti, lower Río Boopi, CAS 59301 (formerly IU 17287), 1 (1, 211.4) [1R]; UMMZ 66434 (formerly IU 17287), 1 (1, 197.8) [1R]. Río Boopi, in San Miguel de Huachi (approximately 14°14′S, 63°41′W), MNHN uncatalogued, 3 (3, 240.8–322.5) [3R]. *Pando:* Río Madre de Dios, 80 km SW of Riberalta, MNHN uncatalogued, 1 (1, 302.4) [1R]. *Santa Cruz:* Santa Cruz, FMNH 78095, 2 (1, 127.4–129.0) [1R]. *Inexact Locality:* Río Mamoré, USNM 310926, 6.

BRAZIL. *Acre:* Vicinity of mouth of Rio Macoma, tributary of Rio Purus, near Sena Madureira (9°04′S, 69°40′W), AMNH 12564, 10 (10, 74.9–122.7). *Amazonas:* Vicinity of mouth of Rio Embira, tributary of Rio Tarauacá, tributary of Rio Juruá, near Envira (7°30′S, 70°15′W), AMNH 12547, 1 (178.3). Near Paraiso, USNM 308033, 1. Paraná de Janauacá, entrance to Lago do Castanho (3°28′S, 60°17′W), USNM 308039, 1; USNM 308082, 1; USNM 308095, 2. Lago Terra Preta, Januari (3°12′S, 60°05′W), USNM 308040, 1; USNM 308047, 1. Ilha da Marchantaria (3°10′S, 59°45′W), USNM 308050, 1; USNM 308065, 3; USNM 308073, 4. Lago Murumuru, USNM 308069, 2. Lago Januari (3°12′S, 60°05′W), MZUSP 6872, 5 (1, 139.9–161.7); USNM 229096, 1; USNM 308041, 1; USNM 308228, 1. Manaus (3°06′S, 60°00′W), MNHN 09.90, 1 (1, 132.8); MZUSP 19292, 2 (1, 213.0–226.8). Rio Negro, Manaus (3°06′S, 60°00′W), MZUSP 6681, 1 (1, 164.0). Tabatinga, MNHN 09.172–173, 2 (1, 113.9–123.1); MNHN 09.174, 1 (1, 94.2). Lago Caial, Tabatinga, MZUSP 27360, 2 (1, 141.7–161.1); MZUSP 27361, 4 (145.5–170.0). Paraná do Lago Amanã, Rio Japurá, Tefé (3°24′S, 64°45′W), MZUSP 27402, 7 (1, 109.1–140.7). Igarapé Cacau, Lago Amanã, mouth of Rio Japurá, MZUSP 36076, 1 (1, 328.1). Lago Maniraná, mouth of Rio Japurá, MZUSP 27925, 1 (1, 155.0). Lago Manacapuru (3°06′S, 61°30′W), MZUSP 6522, 1 (1, 171.4). Lago Jacaré, right shore of Rio Solimões, upriver of Manacapuru (approximately 3°06′S, 61°30′W), MZUSP 6456, 3 (1, 146.9–250.8). Lago Janauacá, Rio Solimões (3°28′S, 60°17′W), MZUSP 1701, 3 (138.6–263.0). Tonantins (2°47′S, 67°47′W), MNHN 09.243–244, 2 (1, 105.3–113.1). Lago on Ilha Amatari, Rio Amazonas, MZUSP 21192, 2 (1, 166.2). Pool on Ilha Sorubim, Rio Solimões, upriver of Coari (approximately 4°05′S, 63°08′W), MZUSP 20935, 4 (4, 77.0–163.3). Mouth of Lago José Açú, Parintins (approximately 2°36′S, 56°44′W), MZUSP 7640, 1 (1, 123.5). Hyavary (=Rio Javari at Brazilian-Peruvian border, approximately 4°22′S, 70°02′W), USNM 119960, 6. Rio Javari just downstream of confluence of Rio Jaquirana and Rio Galvez, NRM 30683, 1. Rio Javari opposite Colonia Angamos, Peru, NRM 30704, 1. Mouth of Rio Içá, município de Santo Antônio do Içá (3°07′S, 67°58′W), MZUSP 27359, 1 (1, 110.4). Igarapé Boa Vista, right margin of Rio Içá, upriver of Cuianá (approximately 3°00′S, 68°01′W), MZUSP 21011, 1 (1, 200.8). Lago Curuçá, below Itacoatiara, MZUSP 13547–48, 2 (1, 304.0–327.8). Itapiranga, Paraná de Urucará (2°32′S, 57°45′W), MZUSP 9561, 2 (1, 150.6–153.5). Urucará, Paraná de Urucará (2°32′S, 57°45′W), MZUSP 5777, 1 (1, 193.3). Igarapé Manduaçu, Paraná de Iupiá, MZUSP 20968, 31 (2, 108.8–196.0). Lago Castro, mouth of Rio Purus (3°51′S, 61°22′W), MZUSP 6302, 5 (1, 176.6–192.0). Rio Içapó, mouth of Rio Jutaí (approximately 2°31′S, 67°22′W), MZUSP 21023, 1 (1, 205.7). Rio Madeira, 25 km below Nova Olinda (approximately 3°45′S, 59°03′W), MZUSP 6956, 1 (1, 146.3). Rio Solimões, BMNH 1925.10.28:63, 1 (1, 334.7). Vicinity of Rio Embira, tributary of Rio Tarauacá, Rio Juruá basin (7°30′S, 70°15′W), USNM 94633, 1. Vicinity of mouth of Rio Macauhan, tributary of Rio Yaco (=Iaco), Rio Purus basin (9°20′S, 69°00′W), USNM 94664, 4. *Goiás:* Rio Macacos, right shore of Rio Paraná, fazenda Fortaleza, município de Flores de Goiás, MZUSP 40387, 1 (147.2). Poço da Gandaia, marginal lagoa of Rio Paraná, fazenda Olho d'água, Flores de Goiás, MZUSP 40456, 15 (2, 82.5–161.3). Lagoa do Embú, right shore of Rio Paraná, bairro Rua Velha, Flores de Goiás, MZUSP 40419, 12 (1, 89.8–133.5). Rio Paraná, fazenda Salobro, 8 km upriver of ferry crossing on highway GO-112, Iaciara, MZUSP 40565, 37 (1, 79.3–128.3); MZUSP 40589, 3 (1, 136.9–150.0). Riacho Estiva, near bridge on highway GO-110, 50 km from São Domingos, MZUSP 40606, 1 (104.2). Rio São Mateus, fazenda Pé do Morro, upriver of bridge on highway GO-110, São Domingos, MZUSP 40616, 3 (87.4–104.5). Rio Araguaia, Aruanã (14°54′S, 51°05′W), MZUSP 4837, 18 (1, 106.3–174.1). Lago das Olarias, near Aruanã, Rio Araguaia (14°54′S, 51°05′W), MZUSP 21541, 1 (228.5). Rio Meninos, at junction with Rio Maranhão, CAS 58883, 1 (161.0). Rio Tiqui, at junction with Rio Maranhão, Rio Tocantins basin, CAS 58893, 1 (154.7). "Fecho" do Rio Paraná, below mouth of Rio São Domingos, Nova Roma, MZUSP 40787, 1 (1, 235.5). Rio Bezerra, right bank tributary of Rio Paraná, 2 km upriver of its mouth, município de Monte Alegre de Goiás, MZUSP 40723, 9 (93.2–120.1). Rio Resende, tributary of Rio Vermelho, approximately 10 km from Buenolândia, MZUSP 26531, 2 (1, 180.0–204.6). *Maranhão:* Marginal lagoa of Rio Tocantins, Estreito, MZUSP 4642–4645, 4 (1, 109.5–128.0). Rio Tocantins, Estreito, MZUSP 4981, 39 (106.3–131.2). *Mato Grosso:* Main channel of upper course of Rio Juruena, USNM 194309, 8 (2, 72.8–98.9) [8R]; USNM 194398, 5. Riacho Monjolinho, tributary to Rio Preto at road to San Francisco, Município de Diamantino (Rio Arinos system of upper Rio Juruena basin), USNM 326727, 1. *Pará:* Rio Tapajós, below Porto Flexal, PARNA, MZUSP 25305, 1 (193.0); MZUSP 25306, 1 (1, 349.8); MZUSP 25477, 1 (114.0). Rio Tapajós, Santarém (2°26′S, 54°42′W), MZUSP 8517, 1 (140.0). Rio Maicá, Santarém (2°26′S, 54°42′W), MZUSP 9173, 1 (1, 235.0). Rio Jamanxim, upriver of Bebal, right bank tributary of Rio Tapajós, outside limits of PARNA, MZUSP 25325, 1 (1, 218.0). Buburé (posto), left bank of Tapajós, km 75 BR-230, PARNA, MZUSP 25564, 1 (1, 267.7). Ilha da Barreirinha, Rio Tapajós, near São Luís (4°10′S, 56°03′W), MZUSP 22098, 6 (1, 165.6–196.0). Lago Santa Clara, Monte Cristo, Rio Tapajós (4°04′S, 55°38′W), MZUSP 22034, 1 (1, 180.1). Rio Trombetas, Oriximiná (1°45′S, 55°32′W), MZUSP 5456, 3 (312.0–323.0); MZUSP 6248, 1 (1, 348.8); MZUSP 8250, 1 (128.0). Lago Paru, Oriximiná (1°45′S, 55°32′W), MZUSP 5597, 2 (2, 290.4–313.2). Rio Tocantins, between Mocajuba and Baião, MZUSP 21262, 4 (117.2–142.8). Rio Tocantins, Baião, MZUSP 21265, 17 (2, 106.5–137.5); MZUSP 21271, 11 (112.8–131.2). Lago along shores of Igarapé Espirito Santo, between Baião and Tucuruí, Rio Tocantins, MZUSP 21275, 3 (1, 129.6–142.8). Marginal lagoa along Rio Tocantins, near Tucuruí (3°42′S, 49°47′W), MZUSP 21297, 31 (102.0–132.1). Igarapé Murú, Rio Tocantins, below Tucuruí (approximately 3°42′S, 49°47′W), MZUSP 21281, 7 (98.1–118.5); MZUSP 21287, 1 (1, 142.1). Small lagoa near Tucuruí, Rio Tocantins (3°42′S, 49°47′W), MZUSP 21332, 1 (1, 123.5). Lagoa in front of Jatobal, Rio Tocantins, MZUSP 21304, 146 (2, 75.5-132.2); MZUSP 21313, 7 (88.8–101.9). Lagoa near Canal do Capitariquara, near Jatobal, Rio Tocantins, MZUSP 21320, 20 (2, 83.1–116.7), MZUSP 42682, 2 (cleared and counterstained for bone and cartilage). Marabá, Rio Tocantins, MZUSP 21466, 1 (1, 161.6). Igarapé Oxipucu, Mocajuba, Rio Tocantins, MZUSP 21258, 9 (1, 99.0–130.0). Paraná Samuuma, mouth of Rio Tocantins, MZUSP 21252, 7 (2, 152.9–177.0). Rio Fresco, aldeia Gorotire, município de São Félix do Xingú, MZUSP 35965, 1 (1, 132.4). Cachoeira do Espelho, Rio Xingú, MZUSP 36857, 3 (2, 201.4–273.2). Furo do Aquiqui, mouth of Rio Xingú, MZUSP 21344, 2 (1, 162.0–171.9). Igarapé Aricurá, Cametá (2°15′S, 49°30′W), MZUSP 21256, 2 (1, 117.5–159.6). Monte Alegre, Rio Amazonas (2°00′S, 54°04′W), MZUSP 9503, 2 (1, 76.7–82.8). Area of Monte Alegre, Rio Maicurú, NRM 19552, 1. Abaetetuba, MZUSP 21239, 4 (1, 149.9–158.7). Igarapé São Lourenço, Furo do Panaquera, MZUSP 21241, 1 (148.3). *Rondônia:* tributary of Rio Madeira, near Porto Velho (approximately 8°46′S, 63°54′W), ANSP 39156, 1 (all counts and measurements taken but not included in ranges for species because of poor condition of specimen, 20.7, holotype of *Curimatus tigris*) [1R]; ANSP 39157–39181, 25 (10.6–22.3, paratypes of *Curimatus tigris*) [25R]; USNM 92957 (formerly ANSP 39185–39186), 2 (14.3–19.8, paratypes of *Curimatus tigris*) [2R]. Rio São Domingos, in Santa Cruz da Serra, Rio Jaru basin MZUSP 28126, 2 (1, 141.6–195.0). *Inexact Locality:* Rios Araguaia and Tocantins, MZUSP 19271, 1 (235.0).

COLOMBIA. *Amazonas:* Río Putomayo drainage at Buenaventura, NRM 30697, 9. Río Amazonas, Puerto Nariño, Finca Merced, NRM 26099, 4. *Caquetá:* Florencia, Río Ortegaza, ANSP 86710, 2 (1, 164.3–170.2). Unnamed river 10–20 mi [16–32 km] upriver of confluence with Río Caguán, CAS-SU 50618, 1 (1, 95.5) [1R]. Small riacho between Tres Esquinas and Río Orteguaza, CAS-SU 50672, 12 (1, 52.4–99.4) [1R]. Río Dedo, tributary of Río Orteguaza, USNM 120178, 1.

ECUADOR. *Napo:* Río Punino, tributary of Río Payamino (approximately 0°27′S, 77°00′W), MCZ 51880, 2 (1, 236.4–249.4) [1R]. Upper portion of Río Tiputini, Río Napo basin, FMNH 97292, 3 (1, 172.0–191.0) [1R]. Lower portion of Río Tiputini, Río Napo basin, FMNH 97293, 4 (1, 89.5–157.6). Laguna Añangucocha, Río Napo basin, FMNH 97291, 1 (1, 193.1). Jatuncocha (1°00′S, 75°27′W), BMNH 1970.4.3:87, 1 (330.6).

PERU. *Huánuco:* Quebrada Pijuayal, tributary of Río Pachitea, near Tournavista, BMNH 1969.7.15:49, 1 (1, 127.9) [1R]. Río Huallaga, near Tingo Maria, ANSP 147880, 1 (1, 233.2) [1R]. Río Yamushimás, tributary of Río Palcazú, tributary of Río Pachitea, near Longin, USNM 290146, 1 (1, 146.6) [1R]. Mouth of tributary to Río Pachitea, 2–3 km downstrean of Tournavista, NRM 30696, 1; NRM 30701, 3. *Junín:* Río Perené, Perené, USNM 53473, 1 (1, 246.1, holotype of *Prochilodus caudifasciatus*) [1R]. *Loreto:* Río Amazonas, across from Pueblo Gallito, 11.5 km SSE of Iquitos (3°48′50″S, 73°09′52″W), INHS 44262, 9 [9R]; INHS 44263, 2 [2R]. Río Nanay, opposite Llanchama Cocha, NRM 30700, 2. Río Nanay, Pampa Chica (3°8′48″S, 73°17′W), INHS 43195, 2. Caño Sacarito, Río Orosa basin (3°36′50″S, 72°16′55″W), INHS 39664, 3. Río Nanay basin, caño Santa Rita (3°45′24″S, 73°17′30″W), INHS 52460, 2. Río Itaya basin, pools near Quebrada Tocón Grande, at km 33 on highway between Iquitos and Nauta, NRM 30654, 1. Río Itaya, 5 to 20 km upstream of Belen (Iquitos) (3°51′S, 73°12′W), USNM 268436, 7. Río Tamshiyacu and adjoining Río Amazonas (4°00′S, 73°09′W), INHS 53238, 1 [1R]. Nauta, confluence of Ríos Marañon and Ucayali, ANSP 21211, 1 (1, 55.1, holotype of *Prochilodus cephalotes*) [1R]; ANSP 21267, 1 (1, 165.9, holotype of *Prochilodus ortonianus*) [1R]. Río Paranapura, in Yurimaguas (5°54′S, 76°05′W), CAS 59305 (formerly IU 17845), 1 (1, 108.1) [1R]. Caño Tuyé, near Pebas (Pevas, 3°20′S, 71°49′W), CAS-SU 36630, 2 (1, 97.2-100.7) [1R]. Caño Shansho, USNM 175838, 1. Río Apayacu, USNM 175843, 1. Supaycocha, Jenaro Herrera, provincia Pequena, MZUSP 26444, 2 (1, 83.4–90.1). Isla Padre, Río Amazonas, Iquitos (3°46′S, 73°15′W), MZUSP 15226, 5 (1, 40.1–50.4). Caño entering Río Manite about 10 km upriver of junction of Río Manite and Río Amazonas (3°32′S, 72°40′W), USNM 280448, 7. Caño entering Río Manite about 8 km upriver of junction of Río Manite and Río Amazonas (3°31′S, 72°40′W), USNM 280435, 10. Iquitos market (3°46′S, 73°15′W), USNM 163847, 3; USNM 280473, 4. Near Petropolis, USNM 261439, 1. Pangacocha, Río Nanay, MZUSP 21363, 1 (1, 123.8). Río Pacaya, MZUSP 4502, 2 (1, 144.4–144.8). Río Otocoro, BMNH 1977.3.10:176–7, 2 (1, 95.8–108.5). Provincia Maynas, Río Napo, Cocha de Conchas (0°59′22″S, 75°18′33″W), USNM 332504, 2. Río Napo basin, Cayapozo, NRM 30725, 9. Río Marañon, below mouth of Río Pastaza, USNM 167791, 2. Río Putomayo, NRM 30693, 1; NRM 30698, 1. Río Samiria, Base Tacsha, left bank sand playa, NRM 30699, 1. *Madre de Dios:* Provincia Manu, Cosha Sandoval, Río Manú, approximately 1.5 bends of river from Pakitza (approximately 11°50′S, 71°15′W), ANSP 142556, 1 (365.7). Provincia Manu, Pakitza, Quebrada Martin Pescador (approximately 11°50′S, 71°15′W), USNM 324271, 2. Provincia Manu, Parque Nacional Manu, Pakitza (approximately 11°50′S, 71°15′W), USNM 327649, 1. Provincia Manu, small pools near Quebrada Pachija (approximately 11°50′S, 71°15′W), USNM 326974, 3. Cocha Tupuhumaro, NW of Puerto Maldonado, Río Madre de Dios, close to confluence with Río de Las Piedras (approximately 12°36′S, 69°11′W), ANSP 142549, 1 (1, 291.5); ANSP 142550, 1 (1, 347.9); ANSP 142594, 1 (1, 322.5). Provincia Manú, mouth of Panahua, where quebrada Panahua enters Río Manú, USNM 302263, 1 (1, 109.0) [1R]. Stream emptying into Río Tambopata, 500 m from Explorer's Inn (approximately 12°49′35″S, 69°17′30″W), USNM 263989, 2 (1, 157.2–165.2) [1R]. Second quebrada emptying into Río Tambopata along shore, SW of mouth of Río La Torre (12°49′40″S, 69°18′W), USNM 263988, 1 (1, 126.4) [1R]. Río Tambopata, stream 200 m upriver of mouth of Río La Torre (~12°50′S, 60°18′W), USNM 263987, 3 (2, 161.0–192.7). Stream on S side of Río Madre de Dios, about 10 km downstream of junction of Río Tambopata and Río Madre de Dios (12°36′S, 69°10′W), USNM 264029, 7. Río Tambopata basin, Quebrada San Roque, at km 11 on road between Puerto Maldonado and Cuzco, NRM 30682, 6. *Ucayali:* Provincia Coronel Portillo, main channel of Río Ucayali, approximately 10 km upriver of Pucallpa, USNM 280447, 22 (2, 87.7–175.8). Provincia Coronel Portillo, Yarinacocha, opposite landing for town of Yarinacocha (8°16′S, 74°36′W), USNM 280609, 4 (1 specimen cleared and counterstained for bone and cartilage). Yarinacocha, AMNH 35706, 1 (105.1); AMNH 35707, 1 (107.8); USNM 280429, 8. Provincia Coronel Portillo Río Neshuya, Neshuya Highway, km 60 on road between Pucallpa and Huanuco (8°17′S, 75°03′W), MZUSP 26652, 3 (31.2–43.1); MZUSP 26653, 3 (1, 77.8–86.4). Provincia Coronel Portillo Lobococha, Masisea (8°36′S, 74°19′W), MZUSP 26066, 4 (3, 36.2–80.0). Provincia Coronel Portillo, Río Ucayali, Bagazan MZUSP 26170, 7 (1, 90.0–120.0). Contamana, Río Ucayali, USNM 167792, 3. Yurimaguas, Río Huallaga (5°54′S, 76°05′W), BMNH 1867.6.13:12, 1 (254.6). Mouth of Río Pachitea (8°46′S, 74°32′W), USNM 163848, 1. Río Ucayali basin, Peru, LIRP 1312, 5 (12.8–13.6 mm BL; 30 day post-spawning preflexion larvae from experimental spawning facility).

Inexact Locality: "Upper Amazon," BMNH 1866.2.15:15–16, 2 (1, 180.1).

Prochilodus reticulatus Valenciennes, 1850

FIGURES 52, 57; TABLE 15

Prochilodus reticulatus Valenciennes in Cuvier and Valenciennes, 1850:92 [type locality: lagune de Maracaïbo (=Venezuela, Lago Maracaibo); common name].—Günther, 1864:295 [in part, Lake of Maracaibo (=Lago Maracaibo); not Kner, 1859, reference or citation of species from Brazil].—Lütken, 1875c:228 [Maracaibo-Söen (=Lago Maracaibo)].—Eigenmann, 1910: 424 [in part, not citation of species from localities outside of Lago Maracaibo basin].—Bertin, 1947:36 [syntype depository].—Fowler, 1950:222 [literature compilation, in part; not citations of occurrence of species outside of Lago Maracaibo or reported distribution outside that basin].—Mago-Leccia, 1967:250 [reported type locality of Caraccas (=Caracas, Distrito Federal, Venezuela) for *Prochilodus asper* Lütken, 1875, questioned and that species placed into synonymy of *Prochilodus reticulatus*]; 1970:31 [Venezuela]; 1972:53, fig. 7 [redescription; Venezuela, Lago Maracaibo basin; *Prochilodus asper* as a synonym]; 1978:5 [Venezuela].—Ringuelet et al., 1967:204 [in part, not cited occurrences of species in localities outside Lago Maracaibo basin].—Espinosa and Gimenez, 1974:1 [Venezuela, Lago Maracaibo; life history and exploitation in fisheries].—Géry, 1977:219 [Venezuela].—Taphorn and Lilyestrom, 1984a:15 [Venezuela].—Petrere, 1989:6 [efficiency of fishery for species].—Menezes and Vazzoler, 1992:62 [reproductive characteristics].—Leon et al., 1993:1 [development].—Ferrer-Montano, 1996:89 [growth, mortality, and recruitment].—Taphorn et al., 1997:79 [Venezuela].—Mojica-C., 1999:554 [Colombia, Río Catatumbo].—Instituto Alexander von Humboldt, 2000:184, 189 [Colombia, Río Catatumbo basin, endangered; transplantation in Colombia].—[Not Kner, 1859:146; Perugia, 1897:25; Magalhães, 1931:111; Pearson, 1937b:109; Fowler, 1940b:98; 1950:222 [in part; not citation of species from Amazonas]; Planquette et al., 1996:132.]

Prochilodus asper Lütken, 1875c:226 (page 37 of separate) [type locality: Caraccas (= Venezuela, Distrito Federal, Caracas), cited type locality questioned by Mago-Leccia (1967:250; 1972:54), restricted herein to Venezuela, Lago Maracaibo].—Steindachner, 1879a:51 [page 35 of reprint; not cited redescription or reported presence of species in Río Magdalena].—Eigenmann and Eigenmann, 1891:48 [in listing of South American fishes].—Eigenmann, 1907b:768 [lateral-line scale count]; 1910:424 [in listing of South American fishes].—Fernández-Yépez and Martin, 1953:33 [cited type locality questioned].—Nielsen, 1974:48 [syntype depository].

Prochilodus reticulatus reticulatus.—Schultz, 1944:261 [recognition as subspecies; Venezuela, Lago Maracaibo basin; common name].—Fowler, 1975: 360 [literature compilation].—Galvis et al., 1997:37, unnumbered figures [Colombia, Lago Maracaibo basin, Río Catatumbo; common name].

Prochilodus reticulatus asper.—Schultz, 1944:261 [shift of *Prochilodus asper* Lütken, 1875c, to subspecies of *P. reticulatus*].

DIAGNOSIS.—The hyaline caudal-fin lobes of *Prochilodus reticulatus* discriminate that species from *P. brevis*, *P. lacustris*, *P. mariae*, *P. nigricans*, and *P. rubrotaeniatus*, which have dark, irregular, wavy, bar-like caudal-fin pigmentation. Among *Prochilodus* species with hyaline caudal fins, *P. reticulatus* differs from *P. vimboides* in the number of scales along the lateral line (41 to 45 versus 34 to 39, respectively) and in the number of horizontal rows of scales around the caudal peduncle (16 to 18 versus 13 to 15, respectively); from *P. britskii* in the number of horizontal rows of scales around the caudal peduncle (16 to 18 versus 13 or 14, respectively) and in the number of teeth in the inner tooth series on each side of the upper jaw (15 to 23 versus 10 to 13, respectively); from *P. argenteus* in the number of horizontal rows of scales between the dorsal-fin origin and the lateral line (7 to 9 versus 10 or 11), the number of vertebrae

FIGURE 57.—*Prochilodus reticulatus*, USNM 121326, 112.3 mm SL; Venezuela, Zulia, small lagoon along Río San Ignacio, approximately 20 km south of Rosario.

(38 to 40 versus 42 to 44, respectively), the number of scales along the lateral line (41 to 45, 43 most frequent, versus 45 to 51, 48 most frequent, respectively), and the number of median predorsal scales (11 to 18, 13 most frequent, versus 17 to 22, 18 most frequent, respectively); from *P. costatus* in the lack of a series of distinct, dark, wavy, horizontal stripes along the lateral surface of the body (versus the presence of such pigmentation in *P. costatus*) and in the number of vertebrae (38 to 40, 39 most frequent, versus 41 to 43, 42 most frequent, respectively); from *P. lineatus* in the lack of a series of distinct, wavy horizontal stripes along the lateral surface of the body (versus the presence of such pigmentation in *P. lineatus*), the number of vertebrae (38 to 40, 39 most frequent, versus 42 to 44, 43 most frequent, respectively), and the number of scales along the lateral line (41 to 45, 43 most frequent and 45 present in only 1 of 30 specimens examined for this feature, versus 44 to 50, 47 most frequent and 45 present in only 3 of 122 specimens examined for this feature, respectively); from *P. hartii* in the number of teeth in the inner row of the lower jaw (8 to 12 versus 13 to 18, respectively), the number of horizontal rows of scales around the caudal peduncle (16 to 18, 17 most frequent and 16 infrequent, versus 14 to 16, 14 and 15 most frequent and 16 infrequent, respectively), and the absence of wavy stripes on the sides of the body (versus the presence of such striping in all but the largest examined specimens); and from *P. magdalenae* in the ranges and modal values of the number of scales along the lateral line (41 to 45, 42 and 43 most frequent, 45 present in only 1 of 30 specimens examined for this feature, versus 43 to 46, 44 and 45 most frequent, respectively; Figure 48), the number of vertebrae (38 to 40, 39 most frequent, versus 39 to 42, 41 most frequent and 39 in only 8% of specimens examined for this feature, respectively; Figure 49), and the number of median predorsal scales (11 to 18, 15 and 16 most frequent, versus 12 to 17, 13 most frequent, respectively; Figure 50).

DESCRIPTION.—Morphometric and meristic data for *Prochilodus reticulatus* presented in Table 15. Body moderately high, transversely compressed. Greatest body depth at dorsal-fin origin. Dorsal profile of head gently concave. Predorsal profile of body moderately convex. Body profile posteroventrally inclined along dorsal-fin base; profile ranging from gently convex to straight between posterior of dorsal-fin base and adipose-fin origin, and concave along caudal peduncle. Predorsal portion of body with slight median ridge. Postdorsal portion of body obtusely rounded transversely. Ventral profile of body moderately convex from tip of lower jaw to posterior of anal-fin base. Ventral profile of caudal peduncle concave. Prepelvic region transversely flattened proximate to pelvic-fin insertion. Distinct median keel present between pelvic-fin insertion and anus.

Head profile pointed. Mouth terminal. Snout length greater than horizontal width of orbit. Nares of each side of head close to each other; anterior nares circular, posterior nares crescent shaped. Adipose eyelid present but poorly developed; most developed anteriorly but with greater part of eye uncovered. Lips fleshy, moderately developed, and forming oral disk when protracted.

Functional teeth in two rows in each jaw. All teeth movably implanted in flesh that overlies jaws. All teeth of similar size, with exposed portions spoon shaped except when worn down. Inner tooth series in each jaw with 15 to 23 teeth on left side of upper jaw and 8 to 12 teeth on left side of lower jaw. Outer row of teeth in each jaw with approximately 103 teeth on each side of upper jaw and approximately 80 teeth on each side of lower jaw in lectotype of *P. asper* (tooth counts in dried lectotype and paralectotypes of *P. reticulatus* impossible to determine). Upper and lower lips bordered by numerous globular, fleshy papillae.

Scales spinoid. Scales in middorsal series between posterior of dorsal-fin base and adipose-fin origin similar in form to those of adjoining portions of body. Lateral line with 41 to 45 (70% of specimens with 43 or 44) scales; 7 to 9 (80.0% of specimens with 8) horizontal rows of scales between dorsal-fin origin and lateral line; 7 or 8 (73.3% of specimens with 7) horizontal rows of scales between pelvic-fin insertion and lateral

TABLE 15.—Morphometrics and meristics of *Prochilodus reticulatus:* (A) lectotype of *Prochilodus reticulatus*, MNHN A.8639 (specimen dried and stuffed with straw); (B) paralectotypes of *Prochilodus reticulatus*, NMNH A.8637–38 and MNHN A.8640 (specimens dried and stuffed with straw); (C) lectotype of *Prochilodus asper*, ZMUC 73; (D) paralectotype of *Prochilodus asper*, ZMUC 72; and (E) all specimens of *Prochilodus reticulatus* from which counts and measurements were taken (morphometric data for lectotype and paralectotypes of *Prochilodus reticulatus* excluded from ranges as a consequence of method of preservation of those specimens; see "Remarks"). Standard length is presented in mm; values 2 to 16 are percentages of SL, 17 to 21 are percentages of HL. Dash indicates missing datum, and question mark indicates specimen damaged for the indicated feature.

Characters	A	B	C	D	E
			Morphometrics		
1. Standard length	278.6	244.3–264.8	191.5	241.5	64.6–278.6
2. Greatest body depth	28.0	28.4–29.9	37.7	36.4	27.8–41.9
3. Predorsal length	39.3	39.2–41.5	43.6	44.4	39.2–48.3
4. Dorsal-fin base length	19.8	17.6–18.3	20.2	19.5	17.6–22.2
5. Dorsal fin to adipose fin distance	28.2	25.0–28.3	27.5	25.7	20.6–28.9
6. Dorsal fin to caudal fin distance	43.5	41.1–43.3	43.8	41.9	39.8–46.5
7. Prepelvic length	47.6	49.2–51.2	50.8	49.0	45.0–56.1
8. Preanal distance	75.8	77.8–79.9	75.7	74.6	72.4–79.9
9. Snout to anal-fin insertion	80.1	81.4–86.0	79.3	78.0	75.1–86.0
10. Anal-fin base length	11.5	9.5–11.0	12.1	12.1	9.4–14.2
11. Caudal-peduncle length	13.2	11.6–13.9	12.8	12.6	11.6–14.9
12. Dorsal-fin length	21.5?	24.2–27.1?	33.9	30.6	27.1–35.2
13. Pectoral-fin length	13.3?	12.5–16.7?	21.0	19.1	19.1–23.6
14. Pelvic-fin length	19.2	14.0–16.4?	21.3	20.6	18.4–26.9
15. Least caudal-peduncle height	10.2	9.9–10.8	12.1	11.9	9.9–12.6
16. Head length	23.2	22.8–24.8	26.5	25.0	22.8–30.8
17. Snout length	39.7	38.0–42.0	40.4	39.1	34.8–44.6
18. Bony orbital diameter	17.8	17.7–40.0	20.9	21.0	17.7–40.0
19. Postorbital length	46.5	39.5–45.5	44.7	43.3	36.5–47.2
20. Interorbital width	52.3	49.4–51.3	54.9	56.8	46.9–58.6
21. Mouth width	41.7	39.8–41.5	43.7	45.8	39.6–48.4
			Meristics		
Lateral-line scales	42	43–44	43	42	41–45
Scale rows between dorsal-fin origin and lateral line	8	8	8	8	7–9
Scale rows between anal-fin origin and lateral line	6	6	7	7	6–7
Scale rows between pelvic-fin insertion and lateral line	8	7–8	8	7	7–8
Rows of scales around caudal peduncle	17	16–18	16	16	16–18
Median predorsal scales	15?	16–18	15	15	11–18
Median scales between dorsal and adipose fins	16	15–16	16	13	12–16
Vertebrae	–	–	39	39	38–40
Inner row teeth, upper jaw	–	–	17	18	15–23
Inner row teeth, lower jaw	–	–	11	9	8–12

line; 6 or 7 (60.0% of specimens with 7) horizontal rows of scales between anal-fin origin and lateral line; 11 to 18 (34.0% of specimens with 13) median predorsal scales; 12 to 16 (48.3% of specimens with 14) scales in middorsal series between posterior of dorsal-fin base and adipose-fin origin; 16 to 19 (56.7% of specimens with 18) horizontal rows of scales around caudal peduncle.

Dorsal fin preceded by small, but well-developed, anteroventrally bifurcate, procumbent spine somewhat triangular in lateral view. Dorsal-fin rays (including procumbent spine) iii,10 [iii,10]; anal-fin rays iii,7 to 9 (iii,8 most frequent) [iii,8]; pectoral-fin rays i,13 to 15 (i,14 most frequent) [i,14]; pelvic-fin rays i,8 [i,8]; principal caudal-fin rays 10/9 [10/9].

Vertebrae 38 to 40 (59.5% of specimens with 39).

Dorsal fin truncate, slightly pointed distally; posterior unbranched and anterior branched rays longest and subequal. Dorsal-fin origin located closer to tip of snout than to caudal-fin base. Greatest length of adipose fin approximately equal to horizontal width of orbit. Adipose-fin origin located along vertical that passes through middle of anal-fin base. Pectoral fin distally pointed. Tip of adpressed pectoral fin reaching posteriorly almost to pelvic-fin insertion. Pelvic fin falcate. Pelvic-fin insertion typically located along vertical that passes though anterior one-fourth of dorsal-fin base. Tip of adpressed pelvic fin reaching, or almost reaching, anus. Axillary scale present, its length approximately one-fourth of greatest length of pelvic fin. Posterior unbranched and anterior branched anal-fin rays longest and subequal. Caudal fin bifurcate.

COLORATION IN ALCOHOL.—Ground coloration silvery yellow, with dorsal portions of body and head darker. Lateral surface of body with up to 12 dark, vertically elongate, diffuse and irregular patches of pigmentation between head and caudal fin. Patches with approximate overall form of narrow isosceles triangles with apexes located along middle of ventrolateral portion of body and bases along dorsomedial region of body. Pigment patches well developed in small specimens, but indistinct or absent in large individuals. Pattern of distinct, wavy, dark, horizontal stripes present on lateral surface of body in many congeners not apparent in examined specimens. Field of black or brown chromatophores forming dark, irregular spot on upper one-half of opercle.

Dorsal fin with 3 to 8 (most frequently 6) dark, irregular stripes beginning on anterior margin of fin and running approximately parallel to dorsal-fin base. Adipose fin with dorsal margin finely bordered with black. Pectoral, pelvic, anal, and caudal fins dusky. Iris yellowish silver, with diffuse dusky dorsal and ventral regions.

COLORATION IN LIFE.—According to Schultz (1944:264), the dorsal fin is pinkish and the sides of the body are yellowish.

DISTRIBUTION.—*Prochilodus reticulatus* is endemic to the rivers of the Lago Maracaibo basin in northwestern Venezuela and northeastern Colombia (Figure 52, triangles).

COMMON NAME.—Bocachico de Maracaibo (Venezuela).

BIOLOGY AND FISHERIES.—Espinosa and Gimenez (1974) discussed the biology of this species and reported that in the southwestern portion of the Lago Maracaibo basin *Prochilodus reticulatus* is heavily exploited in commercial fisheries.

COMPARISONS.—Differences in various pigmentation and meristic features unequivocally distinguish *Prochilodus reticulatus* of the Lago Maracaibo basin from all of its congeners except for *P. magdalenae,* the only other *Prochilodus* species with a Trans-Andean distribution. The two nominal forms differ in the ranges and modal values of the number of scales along the lateral line, the number of medial predorsal scales, and the number of vertebrae (see "Diagnosis," above, and Figures 48 to 50). In light of these differences and their disjunct areas of occurrence, these two nominal forms are treated as separate species herein.

REMARKS.—Valenciennes (1850:92–93) based his description of *Prochilodus reticulatus* upon six specimens collected by Plée in Lago Maracaibo, Venezuela. The four known extant syntypes at MNHN are dried specimens stuffed with straw. Of these, we herein designate MNHN A.8639, 278.6 mm SL, the syntype in the best overall condition, as the lectotype of *Prochilodus reticulatus*. The three other syntypes (MNHN A.8640, 1 specimen, 264.8 mm SL; and MNHN A.8637–38, 2 specimens, 244.3–248.2 mm SL) consequently become paralectotypes.

Lütken's (1875c:226–229) description of *Prochilodus asper,* was based upon material sent by Villars from Caraccas (= Caracas, Distrito Federal), Venezuela. Mago-Leccia (1972:54) deduced that, although the types were apparently dispatched from Caracas, they probably originated in the Lago Maracaibo system of northwestern Venezuela. That basin is completely separate from, and a significant distance to the west of, the river systems in Caracas, and, furthermore, prochilodontids are apparently absent from the drainage systems in Caracas (Mago-Leccia, 1967; 1972, fig.3; this study). We are unable to distinguish *Prochilodus asper* from *P. reticulatus* (see Table 15) and consequently consider *P. asper* to be a junior synonym of the latter species as previously proposed by Mago-Leccia (1972:53). The conspecificity of the two nominal forms and the evident limitation of *P. reticulatus* to the Lago Maracaibo basin, as attested to by extensive collecting efforts in northern and western Venezuela, lead us to concur with Mago-Leccia's suggestion (1972:53) that the typeseries of *P. asper* undoubtedly originated in the Lago Maracaibo basin rather than at the stated locality of Caracas, which was most likely the transhipment location.

Prochilodus asper is represented by two syntypes in the Kobenhaveens Universitet Zoologisk Museum. We herein designate the syntype in the best condition (ZMUC 73, 191.5 mm SL) as the lectotype of *Prochilodus asper,* and the second syntype of the species (ZMUC 72, 241.5 mm SL) consequently becomes a paralectotype. A specimen of *P. reticulatus* in the collections of NMW (56635) has the same collection data as, and is in a condition similar to, the lectotype (ZMUC 73) and paralectotype (ZMUC 72) of *P. asper*. Steindachner exchanged specimens with Lütken (B. Herzig, NMW; pers. comm., 1987), and it is possible that the NMW specimen is part of the type series of *Prochilodus asper.*

Schultz (1944:261–265) considered *P. reticulatus, P. asper,* and *P. magdalenae* to be subspecies of *P. reticulatus*. The results of our studies indicate that *P. magdalenae* is distinct from *P. reticulatus* and endemic to the Ríos Atrato, Sinú, and Cauca-Magdalena, all in northwestern Colombia. *Prochilodus reticulatus,* in turn, is endemic to the Lago Maracaibo basin of northwestern Venezuela and northeastern Colombia, with *P. asper* as a junior synonym (see "Diagnosis" and Figures 48–50 for differences between *P. reticulatus* and *P. magdalenae*).

Planquette et al. (1996:132) reported *Prochilodus reticulatus* from the western portion of French Guiana, perhaps following the citation of Le Bail et al. (1984:59) of the species from that department of France. *Prochilodus reticulatus* is, however, endemic to the Lago Maracaibo basin of northwestern South America. Because of the lack of an included photograph in the publication by Planquette et al. (1996:134) it is impossible to definitely identify the form that was identified as *P. rubrotaeniatus* by those authors. Nonetheless, all examined *Prochilodus* samples from the region in which the specimens of Planquette et al. were collected, the Marowijne River–Fleuve Maroni system along the French Guiana–Suriname border, have proved to be *P. rubrotaeniatus*. We, thus, consider the specimens that Le Bail et al. (1984) and Planquette et al. (1996) identified as *P. reticulatus* to be *P. rubrotaeniatus*.

MATERIAL EXAMINED.—77 specimens (30, 64.6–278.6 mm SL; partial meristic data taken from additional 25 specimens).

VENEZUELA. *Trujillo:* Río Jimelles, tributary Río Motatán, 12 km E of Motatán, USNM 121332, 1 (1, 201.5) [1R]. Río Motatán, bridge 22 km N of Motatán, USNM 121327, 1 (1, 175.1) [1R]. *Zulia:* Encontrados, FMNH 6335, 3 (1, 171.3–191.4) [4R]. Lago Tulé, approximately 75 km W of Maracaibo, 5 km from Río Socuy, USNM 121330, 2 (2, 130.5–157.5) [2R]. Río Socuy, approximately 3 km upriver of its mouth, USNM 121328, 9 (4, 64.6–203.5) [2R]. Small lagoon along Río San Ignacio, approximately 20 km S of Rosario, USNM 121326, 4 (2, 110.9–115.2) [2R]. Río Apón, approximately 35 km S of Rosario, USNM 121331, 6 (4, 198.3–246.5) [4R]. Caño 0.5 mile (0.8 km) W of Sinamaica, USNM 121329, 2 (2, 203.8–212.8) [2R]. Río Palmar near Totumo, approximately 100 km SW of Maracaibo, USNM 121324, 31 (2, 118.2–243.5) [15R]. Río Negro, near to its confluence with Río Yasa, USNM 121333, 10 (3, 106.0–219.0) [10R]. *Inexact Locality:* Lago Maracaibo, MNHN A.8637–38, 2 (2, 244.3–248.2, paralectotypes of *Prochilodus reticulatus*); MNHN A.8639, 1 (1, 278.6, lectotype of *Prochilodus reticulatus*); MNHN A.8640, 1 (264.8, paralectotype of *Prochilodus reticulatus*). "Caracas" (probably from Lago Maracaibo, see "Remarks," above), BMNH 1876.1.10:25, 1 (165.1); NMW 56635, 1 (1, 212.4; possible paralectotype of *Prochilodus reticulatus,* see "Remarks," above) [1R]; ZMUC 72, 1 (1, 241.5, paralectotype of *Prochilodus asper*) [1R]; ZMUC 73, 1 (191.5, lectotype of *Prochilodus asper*) [1R].

***Prochilodus rubrotaeniatus* Jardine, 1841**

FIGURES 52, 58; TABLE 16

Prochilodus rubrotaeniatus Jardine, 1841:258, pl. 28 [type locality: Rios Branco and Negro as in the Essequibo and its tributaries (=Brazil, Roraima, Rio Branco, Amazonas, Rio Negro; Guiana, Río Essequibo and tributaries). Restricted herein to Rio Branco, Brazil, and Essequibo River, Guiana].—Valenciennes in Cuvier and Valenciennes, 1850:89 [based upon Jardine, 1841].—Günther, 1866:30 [Amazon].—Eigenmann and Eigenmann, 1891:48 [in listing of South American fishes].—Eigenmann and Ogle, 1907:5 [cited similarity to *P. beani*].—Eigenmann, 1907b:768 [lateral-line scale count]; 1910:424 [in listing of South American fishes]; 1912:270 [British Guiana (=Guyana), Essequibo River]; 1922a:116 [comparison with *Prochilodus steindachneri*].—Cockrell, 1914:96 [scale morphology].—Eigenmann and Allen, 1942:309 [comparison with *P. nigricans*].—Fowler, 1945:124 [in part, not cited occurrence of species in Peru]; 1950:223 [literature compilation; in part, not reported occurrence of species in Peru]; 1975:360 [literature compilation].—Boeseman, 1952:184 [Suriname: Coppenam River, Lucie River; common name].—Lowe-McConnell, 1964:110 [Guyana, Rupununi District, north and south savannas of Essequibo River basin, Jacare River of Rio Amazonas basin]; 1984:143 [economic importance].—Fernández-Yépez, 1969:55 [questionably cited as present in Venezuela, Río Caroni].—Mago-Leccia, 1970:26 [Venezuela]; 1972, figs. 5c, 8 [redescription of species; Venezuela, Río Cuyuni and Río Caroní]; 1978:5 [Venezuela].—Géry, 1977:218 [in part, not citation from upper Amazon].—Le Bail et al., 1984:59 [French Guiana].—Ferreira et al., 1988:343 [Brazil, Roraima, Rio Mucujaí].—Lasso et al., 1990:141 [Venezuela, Lago de Guri].—Novoa et al., 1990:159 [Venezuela, Lago de Guri].—Menezes and Vazzoler, 1992:62 [reproductive characteristics].—Taphorn et al., 1997:79 [Venezuela].—Williams and Winemiller, 1998:281 [Venezuela, Guri Reservoir; dominance of species in gill-net surveys].—Machado-Allison et al., 2000:17 [Venezuela, Río Cuyuni, Raudal de Paruruvaca].—[Not Günther, 1864:295.]

Prochilodus cf. *nigricans*.—Goulding et al., 1988:129 [Brazil, Rio Negro].

Prochilodus nigricans [not of Agassiz, 1829].—Günther, 1864:295 [in part, *Prochilodus rubrotaeniatus* incorrectly placed as synonym of *P. nigricans* Agassiz, 1829; Guyana, Essequibo River].

Prochilodus maripicru Eigenmann, 1912:271, pl. 35: fig. 2 [type locality: British Guiana (=Guyana), Essequibo, Maripicru Creek, a branch of Ireng (River, Amazon basin)].—Boeseman, 1953:13 [Suriname, Marowini River basin; common name].—Mago-Leccia, 1972:47 [use of caudal-fin pigmentation to distinguish species groups].—Géry, 1977:219 [Guianas].—Ibarra and Stewart, 1987:70 [type depository].—[Not Ovchynnyk, 1971:105.]

Prochilodus reticulatus [not of Valenciennes, 1850].—Le Bail et al., 1984:59 [French Guiana].—Planquette et al., 1996:132 [western portions of Guyane (=French Guiana)].

Prochilodus cf. *rubrotaeniatus*.—Ferreira et al., 1988:343, table 1 [Brazil, Rio Branco basin].

DIAGNOSIS.—The dark, irregular, wavy, bar-like patterns on the caudal-fin lobes of *Prochilodus rubrotaeniatus* distinguishes that species from *P. argenteus, P. britskii, P. costatus, P. hartii, P. lineatus, P. magdalenae, P. reticulatus,* and *P. vimboides,* which have hyaline caudal fins. Within the group of *Prochilodus* species with dark caudal-fin markings, *P. rubrotaeniatus* differs from *P. mariae* in the number of scales along the lateral line (44 to 48 scales versus 52 to 64, respectively) and in the number of dark, wavy, horizontal stripes along the lateral surface of the body dorsal to the lateral line (3 to 5 versus 6 or 7, respectively); from *P. lacustris* in the form of the scales (with complex pattern of variable subdivisions versus having only radial subdivisions) and in the number of horizontal rows of scales between the pelvic-fin insertion and the lateral line (6 or 7, 6 most frequent, versus 8 to 11, 9 most frequent, respectively); from *P. brevis* in the form of the scales (with complex pattern of variable subdivisions versus having only radial subdivisions) and in the number of horizontal rows of scales between the pelvic-fin insertion and the lateral line (6 or 7, 6 most frequent, versus 6 to 8, 7 most frequent and 6 in only 2% of specimens examined for this feature, respectively); and from *P. nigricans* in the number of horizontal rows of scales around the caudal peduncle (14 to 18, with 16 most frequent and 17 and 18 in only 10.8% of specimens examined for this feature, versus 17 to 21, with 19 most frequent and 17 in only 0.9% of specimens examined for this feature, respectively; Figure 54), the number of horizontal rows of scales between the pelvic-fin insertion and the lateral line (6 or 7, 6 most frequent, versus 7 to 9, 8 most frequent, respectively; Figure 55), and the range and modal numbers of lateral-line scales (44 to 48 with 45 most frequent and 47 and 48 in only 10% of specimens examined for this feature, versus 44 to 51 with 49 most frequent and 44 to 46 in only 3.0% of specimens examined for this feature, respectively; Figure 56).

DESCRIPTION.—Morphometric and meristic data for *Prochilodus rubrotaeniatus* presented in Table 16. Body comparatively high, transversely compressed. Greatest body depth at dorsal-fin origin. Dorsal profile of head moderately concave. Predorsal profile of body convex. Body profile posteroventrally inclined along dorsal-fin base; profile straight from pos-

TABLE 16.—Morphometrics and meristics of *Prochilodus rubrotaeniatus:* (A) holotype of *Prochilodus maripicru,* FMNH 53597; and (B) all specimens of *Prochilodus rubrotaeniatus* from which counts and measurements were taken. Standard length is presented in mm; values 2 to 16 are percentages of SL, 17 to 21 are percentages of HL.

Characters	A	B
	Morphometric	
1. Standard length	236.2	69.9–320.8
2. Greatest body depth	32.1	31.4–42.4
3. Predorsal length	46.1	42.7–48.4
4. Dorsal-fin base length	15.5	15.5–20.7
5. Dorsal fin to adipose fin distance	27.6	23.4–30.6
6. Dorsal fin to caudal fin distance	42.4	39.1–48.1
7. Prepelvic length	50.1	47.4–55.7
8. Preanal distance	77.6	75.4–83.0
9. Snout to anal-fin insertion	81.2	77.7–86.9
10. Anal-fin base length	10.2	9.7–13.2
11. Caudal-peduncle length	11.7	11.4–14.9
12. Dorsal-fin length	27.4	27.3–40.2
13. Pectoral-fin length	19.3	19.3–25.0
14. Pelvic-fin length	17.9	17.9–26.1
15. Least caudal-peduncle height	11.4	10.6–13.9
16. Head length	24.0	24.0–33.8
17. Snout length	46.6	33.1–46.6
18. Bony orbital diameter	23.1	19.1–32.0
19. Postorbital length	38.8	35.5–43.2
20. Interorbital width	52.0	48.1–60.7
21. Mouth width	44.4	37.8–53.2
	Meristics	
Lateral-line scales	45	44–48
Scale rows between dorsal-fin origin and lateral line	8	7–9
Scale rows between anal-fin origin and lateral line	5	5–7
Scale rows between pelvic-fin insertion and lateral line	6	6–8
Rows of scales around caudal peduncle	16	14–18
Median predorsal scales	14	13–17
Median scales between dorsal and adipose fins	16	14–18
Vertebrae	42	41–42
Inner row teeth, upper jaw	18	16–23
Inner row teeth, lower jaw	11	9–13

terior of dorsal-fin base to adipose-fin origin, and concave along caudal peduncle. Predorsal portion of body with slight median ridge. Postdorsal portion of body obtusely rounded transversely. Ventral profile of body convex from tip of lower jaw to posterior of anal-fin base. Ventral profile of caudal peduncle concave. Prepelvic region transversely flattened proximate to pelvic-fin insertion. Distinct median keel present between pelvic-fin insertion and anus.

Head profile pointed. Mouth terminal. Snout length much greater than horizontal width of orbit. Nares of each side of head close to each other; anterior nares circular, posterior nares crescent shaped. Adipose eyelid present but poorly developed; most developed anteriorly, but with greater part of eye uncovered. Lips fleshy, moderately developed, and forming oral disk when protracted.

Functional teeth in two rows in each jaw. All teeth movably implanted in flesh that overlies jaws. All teeth of similar size and spoon shaped except when worn down. Inner tooth series with 16 to 23 teeth on left side of upper jaw and 9 to 13 teeth on left side of lower jaw. Outer row of teeth in each jaw with approximately 94 teeth on each side of upper jaw and approximately 87 teeth on each side of lower jaw in examined type specimens. Upper and lower lips bordered by numerous globular, fleshy papillae.

Scales spinoid. Scales in middorsal series between posterior of dorsal fin and adipose-fin origin similar in form to those of adjoining regions of body. Lateral line with 44 to 48 (41.2% of specimens with 46) pored scales; 7 to 9 (88.2% of specimens with 8) horizontal rows of scales between dorsal-fin origin and lateral line; 6 or 7 (55.9% of specimens with 6) horizontal rows of scales between pelvic-fin insertion and lateral line; 5 to 7 (74.3% of specimens with 6) horizontal rows of scales between anal-fin origin and lateral line; 13 to 17 (55.9% of specimens with 14) median predorsal scales; 14 to 18 (35.3% of specimens with 16) scales in middorsal series between posterior of dorsal-fin base and adipose-fin origin; 14 to 18 (32.4% of specimens with 16) horizontal rows of scales around caudal peduncle.

Dorsal fin preceded by small, but well-developed, anteroventrally bifurcate, procumbent spine somewhat triangular in lateral view. Dorsal-fin rays (including procumbent spine) iii,7 to 10 (iii,7 very rare) [11 rays reported by Jardine in original description, a count that presumably includes both branched and unbranched rays]; anal-fin rays ii,8 or iii,8 (iii,8 most frequent) [10 rays reported by Jardine in original description, a count that presumably includes both branched and unbranched rays]; pectoral-fin rays i,13 to 16 (i,14 most frequent) [15 rays reported by Jardine in original description, a count that presumably includes both branched and unbranched rays]; pelvic-fin rays i,8 or 9 (i,8 most frequent) [9 rays reported by Jardine in original description, a count that presumably includes both branched and unbranched rays]; principal caudal-fin rays 10/9.

Vertebrae 41 or 42 (60.0% of specimens with 41) [40 vertebrate reported by Jardine in original description; see "Remarks"].

Dorsal fin truncate, slightly pointed distally; posterior unbranched and anterior branched rays longest. Dorsal-fin origin located closer to tip of snout than to caudal-fin base. Greatest length of adipose fin approximately equal to horizontal width of orbit. Adipose-fin origin located along vertical that passes through anterior one-third of length of anal-fin base. Pectoral fin pointed distally. Tip of adpressed pectoral fin reaching, or almost reaching, pelvic-fin insertion. Pelvic fin falcate. Pelvic-fin insertion located along vertical that passes through anterior one-third of dorsal-fin base. Tip of adpressed pelvic fin reaching approximately two-thirds of distance between pelvic-fin insertion and anus. Axillary scale present, its length approximately one-fourth of greatest length of pelvic fin. Posterior unbranched and anterior branched anal-fin rays longest and subequal. Caudal fin moderately bifurcate.

COLORATION IN ALCOHOL.—Ground coloration silvery yellow or brownish yellow, with dorsal portion of body and head darker. Lateral surface of body with 10 to 24 dark, vertically

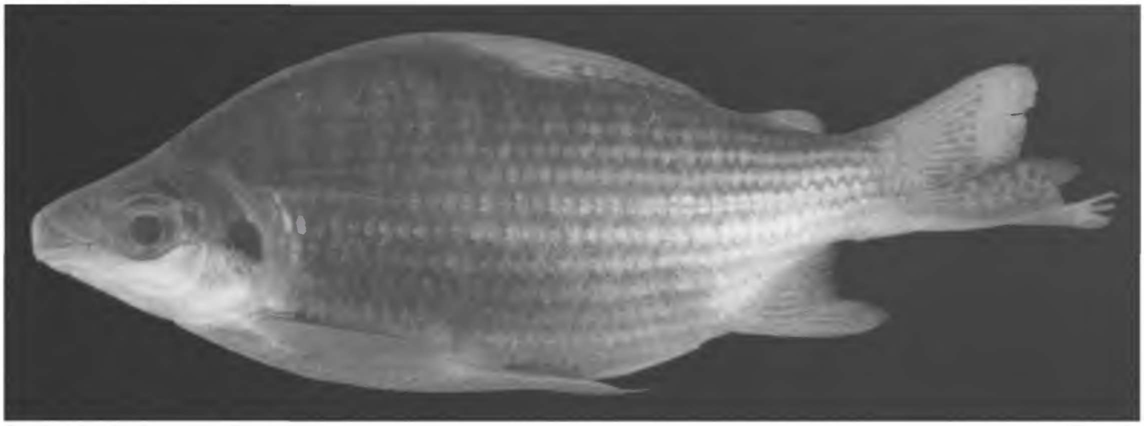


FIGURE 58.—*Prochilodus rubrotaeniatus*, USNM 225419, 150.4 mm SL; Suriname, Marowijne, Corantjin River at km 180, side channel of main river along Surinamese shore.

elongate, diffuse, and irregular patches of pigmentation between head and caudal fin. Patches with approximate overall form of narrow isosceles triangles, with apex located along middle of ventrolateral portion of body and base on dorsomedial region of body. Pigment patches well developed in small specimens, but indistinct or absent in large individuals. Lateral surface of body with approximately 8 to 12 dark, wavy, horizontal stripes along dorsal and ventral margins of exposed portions of scales. Approximately 3 to 5 (most frequently 4) wavy stripes dorsal to, and 5 to 7 (most frequently 6) wavy stripes below, lateral line. Field of black or brown chromatophores forming dark, irregular spot on upper one-half of opercle.

Dorsal fin with 4 to 10 (most frequently 5) dark irregular stripes beginning on anterior margin of fin and extending across fin approximately parallel to base of fin. Adipose fin with dorsal margin finely bordered with black. Pectoral, pelvic, and anal fins dusky. Caudal fin with 2 to 5 (most frequently 3) irregular vertical bars and wavy patterns formed of small dark spots made of groups of chromatophores. Iris yellowish silver or brownish silver, with diffuse, dusky dorsal and ventral regions.

COLORATION IN LIFE.—(Based upon a photo of what is apparently a specimen in an aquarium published in Planquette et al. (1996:133) that was identified by those authors as *Prochilodus reticulatus*. See comments under "Remarks," below, concerning that identification). Overall coloration silvery, more so on ventral portions of head and body, somewhat more dusky dorsally, particularly on dorsal portion of head. Dark pigmentation along scale margins forming irregular horizontal stripes along ventral portions of body. Pelvic fin, distal portions of anal fin, and posterior margin of lower lobe of caudal fin with reddish cast. Upper portion of operculum yellowish. According to Lasso et al. (1990:151), *P. rubrotaeniatus* is light brown with a yellowish coloration in life.

DISTRIBUTION.—Examined specimens of *Prochilodus rubrotaeniatus* originated in the Rio Branco and Rio Marauiá basins, Brazil, and in coastal rivers of Guyana, Suriname, and French Guiana (Figure 52, diamonds). Mago-Leccia (1972:57), Lasso et al. (1990:151), Williams and Winemiller (1998:281), and Machado-Allison et al. (2000:17) also reported the species as occurring in Venezuela in the Río Cuyuni and Río Caroni basins.

COMMON NAME.—Curimatá (Brazil), Bocachica de Guianas (Venezuela); coulitata, courimata, colmata, coumata, koulimata, koumata (French Guiana); koonoomatta, alumassee (Suriname).

COMPARISONS.—The combination of differences in pigmentation and various meristic features unequivocally discriminate *Prochilodus rubrotaeniatus* from all of its congeners with the exception of *P. nigricans*. *Prochilodus rubrotaeniatus* and *P. nigricans* have allopatric distributions (Figure 52) and apparently inhabit different water types (black and clear waters versus white waters, respectively). Furthermore, the two species have minimal overlap in the number of horizontal rows of scales around the caudal peduncle (Figure 54), differ modally in the number of horizontal rows of scales between the pelvic-fin insertion and lateral line (Figure 55), and differ in the number of lateral-line scales (Figure 56). The two nominal forms are consequently herein recognized as distinct species.

REMARKS.—We were unable to locate the type series of *Prochilodus rubrotaeniatus* described by Jardine (1841:258-259, pl. 28). The material had been colllected by Schomburgk in the Rios Branco and Negro, in Brazil, and the Essequibo River, in Guiana. Similarly, no type specimens for the species were reported by Eschmeyer et al. (in Eschmeyer, 1998:1484). Despite the lack of a type series, it is clear from Jardine's original description (1841) that *P. rubrotaeniatus* is the species identified by that name herein. Many previous authors have cited the authorship of this species as either Schomburgk or

Jardine and Schomburgk in Schomburgk. Although the specimens, illustrations, and natural history notes that served as the basis for the description were collected and prepared by Schomburgk, there is no indication from the published text that he collaborated with Jardine in the formal description of the species. We consequently follow Kullander and Stawikowski (1997) and Stawikowski and Kullander (1997) in considering Jardine to be the author of the species.

Only limited samples of *Prochilodus rubrotaeniatus* from the Amazon basin have been examined, and all of those were from the middle and upper portions of the Rio Negro system, the major left bank, black-water tributary to the main Amazon. Most of the examined material from the Rio Negro basin were collected in southwestern Guyana and the northern region of the state of Roraima, Brazil, which are all in the upper portions of the Rio Branco, the major left bank tributary of the Rio Negro (see Figure 52). In addition to these population samples that originated in the Rio Branco drainage, a system proximate to the primary region of occurrence of the species in the Atlantic drainages of the Guianas, a single specimen from the Rio Negro basin proper and another specimen from a tributary stream, the Rio Marauía, have been located (see "Material Examined"). Goulding et al. (1988:100) similarly noted that their extensive sampling along the main stream of the Rio Negro failed to yield samples of *Prochilodus* despite the frequent occurrence of *Semaprochilodus* species through that basin. Those authors (Goulding et al., 1988:100) further remarked that the absence of various otherwise widespread species and genera in the acidic black waters of the Rio Negro system "suggests that Rio Negro hydrochemistry is inimical to some species." The presence of *P. rubrotaeniatus* in the Rio Marauiá also is noteworthy because that river, although a tributary of the black-water Rio Negro, is a clear-water system that drains from the uplands of the Guiana shield (Goulding et al., 1988:42). Although a correlation between clear waters and the areas of occurrence of *P. rubrotaeniatus* apparently applies in the Rio Negro and Rio Branco basins, in Suriname that species occurs in black waters, albeit primarily in tributary rain forest streams rather than the main river channel (pers. observ., second author).

It appears that the *Prochilodus* populations in the black- and clear-water rivers that drain the ancient Guiana shield (Rios Branco and Marauiá in the Amazon basin and the Ríos Caroni and Cuyuni in the north to the Fleuve Oyapock in the south in the Guianas) are isolated from *P. nigricans*, an inhabitant of Amazonian white waters, by different preferences for and/or toleration of, black and clear versus white waters.

Prochilodus maripicru was described by Eigenmann (1912: 271, pl. 35: fig. 2) on the basis of a holotype and two cotypes (=paratypes) that originated in the Ireng River of Guiana, a tributary of the upper Rio Branco of the Amazon basin. As can be seen in Table 16, there are no differences between the type series of *P. maripicru* and examined population samples of *P. rubrotaeniatus*. The morphometric and pigmentary features of *P. maripicru* cited by Eigenmann (1912:271) as distinguishing that nominal form from *P. rubrotaeniatus* all fall within the range of ontogenetic variation in these features for the latter species. Because of the lack of distinguishing features, *P. maripicru* is consequently considered to be a junior synonym of *P. rubrotaeniatus*.

In so far as all of the extremely limited Amazonian samples of *P. rubrotaeniatus* examined in this study originated in tributaries to the Rio Negro, all citations of that species from other portions of the Amazon basin are considered to refer to *P. nigricans*, a morphologically very similar species (see "Diagnosis").

The citation by Le Bail et al. (1984:59, fig. 3b) of *Prochilodus reticulatus* from French Guiana is considered to be erroneous because *P. reticulatus* is endemic to the Lago Maracaibo basin of northwestern South America. Planquette et al. (1996:133) provided a life photograph of a specimen, presumably from French Guiana, that they identified as *Prochilodus reticulatus*. The illustrated specimen has the distinct dark pigmentation pattern on the caudal fin that is absent in *P. reticulatus* but that occurs in *P. rubrotaeniatus*, a species that inhabits that region; consequently, that record is considered to refer to *P. rubrotaeniatus*.

MATERIAL EXAMINED.—130 specimens (32, 69.9–320.8 mm SL; partial meristic data taken from 40 additional specimens).

BRAZIL. *Amazonas:* Rio Marauiá, beach at Cachoeira do Bicho-Açu (0°20′S, 65°20′W), USNM 233849, 1 (1, 107.7) [1R]. *Roraima:* Rio Mucajaí, S of Boa Vista, MZUSP 20722, 2 (2, 101.5–126.4).

GUYANA. *Essequibo:* quiet water area in stream with sandy bottom, Rupununi River, BMNH 1972.7.27:424–426, 3 (1, 217.0–288.0). Kasuero Karanambo, Pirara Stop-off, along margin of Takatu River (Rio Amazonas basin), BMNH 1972.7.27: 428–430, 3 (1, 164.4–227.6) [1R]. Kbo, Rupununi River (Essequibo River basin), BMNH 1972.7.27:431–434, 4 (1, 109.2–214.5) [1R]. Cajuero, Rupununi River, BMNH 1972.7.27: 420–423, 4 (2, 72.2–78.9). Pond 3 mi [4.8 km] N of Yapukarri, Rupununi River, MCZ 48543, 1 (1, 120.9) [1R]. Small pond 5 mi [8 km] N of Manari Ranch, MCZ 48542, 1 (1, 106.8) [1R]. Rockstone, Essequibo River, AMNH 14436, 1 (1, 99.2) [1R]. Sandbar in Rockstone, Essequibo River, CAS 59314 (formerly IU 12254), 3 (1, 195.6–222.3) [1R]. Essequibo River, BMNH uncatalogued, 1 (1, 173.3) [1R]; MNHN 6266, 1 (280.4). Sandbar along N shore of Cuyuni River, directly W of Caouri (Caowry) Creek, AMNH 72138, 4 (1, 144.0–177.2) [1R]. Sandbar along N shore of Cuyuni River, immediately upriver of Caouri (Caowry) Creek, AMNH 72138, 4 (143.9–174.3); AMNH 73004, 1 (1, 103.4) [1R]. Creek near Penal Settlement, Mazaruni River, BMNH 1934.9.12:348–350, 3 (3, 110.7–320.8). Manari River, Manari Ranch, near Lethem, CAS 16068, 1 (100.0) [1R]. Maripicru Creek, branch of Ireng River, FMNH 53597, 1 (1, 236.2, holotype of *Prochilodus maripicru*, formerly CM 2066) [1R]. *Inexact Locality:* Sandbar in Maxiprica, CAS 59315, 1 (1, 165.5) [1R].

FRENCH GUIANA. *Cayenne:* Fleuve Oyapock, Rapides Trois Sauts (2°15'N, 52°53'W), MNHN 1981-398, 1 (1, 120.9).

SURINAME. *Marowijne:* Litani and Oelemari Rivers, AMNH 16405, 1 (1, 302.1) [1R]. *Nickerie:* N shore tributary to Sisa Creek, approximately 700 m upriver of crossing of road between Amotopo and Camp Geology (3°42'N, 57°42'W, USNM 225384, 8 (1, 72.1–90.8) [1R]. Stream at km 212 along road from Amotopo to Camp Geology, in Machine Park (3°50'N, 57°34'W), USNM 225418, 1 (1, 141.3) [1R]. Kamp Kreek, 100 m N of turnoff to Camp Geology (44°9'N, 057°28'W), USNM 225385, 14 (1, 76.1–91.3) [1R]. Corantjin River at km 180, side channel of main river along Surinamese shore (5°08'N, 57°18'W), USNM 225419, 27 (4, 69.9–150.4). Pool in front of Camp Hydro (3°42'N, 57°58'W), AMNH 54936, 4 (79.0–122.6); USNM 225322, 1 (1, 91.2) [1R]. Streams entering Corantjin River at approximately km 385, slightly N of Tiger Falls (4°00'N, 58°02'W), USNM 225323, 1 (1, 81.0) [1R]. Corantijn River, BMNH 1981.6.9:814–815, 2 (1, 102.5–105.0). Kapoeri Creek, approximately 7 km from junction with Corantijn River, AMNH 45770, 13 (77.6–107.8). Stream near Camp Avanavero, approximately 3 mi (4.8 km) downstream of DeVis Falls, AMNH 54845, 17 (89.0–108.6).

***Prochilodus vimboides* Kner, 1859**

FIGURES 52, 59; TABLE 17

Prochilodus nigricans [not of Agassiz, 1829].—Kner, 1859:146 [Brazil, Ypanema].—Nomura, 1984:54 [Brazil, common name].

Prochilodus vimboides Kner, 1859:148 (page 12 of separate), pl. 2: fig. 4 [type locality: Ypanema, Brazil, restricted herein to São Paulo, Ipanema (Varnhagen), Rio Sorocaba basin].—Günther, 1864:294 [based upon Kner 1859].—Steindachner, 1874:533 [description; Brazil, Rio Parahyba (= Paraíba), Rio Mucuri, Rio Doce].—Eigenmann and Eigenmann, 1891:48 [in listing of South American fishes].—Ulrey, 1895:259 [Brazil].—Fowler, 1906:311 [relationship with *Prochilodus steindachneri*]; 1950:225 [literature compilation]; 1975:360 [literature compilation].—Eigenmann, 1907b:768 [lateral-line scale count]; 1910:424 [in listing of South American fishes].—Eigenmann and Ogle, 1907:5 [Brazil].—Pellegrin 1909a:148 [Brazil, Rio Grande].—Mago-Leccia, 1972:47 [use of caudal-fin pigmentation to distinguish species groups].—Britski, 1972:83 [Brazil, Rio Paraná and Rio Paraíba basins].—Godoy, 1975:810 [Brazil, Rio Mogi-Guassu basin; biology].—Ringuelet, 1975:59 [Rio Paraná].—Géry, 1977:219 [(Brazil), Rio Parahyba (= Paraíba)].—Böhlke, 1984:148 [as possible senior synonym of *P. steindachneri*, evidently following Géry, 1977].—Britski et al., 1984:59 [Brazil, Rio São Francisco].—Nomura, 1984:54 [Brazil, common name].—Pauls and Bertollo, 1984:787 [karyotype].—Northcote et al., 1985:2707 [effects of impoundment on populations of species].—Bertollo et al., 1986:156, table 1 [karyotype].—Britski et al., 1986:59 [Brazil, Rio São Francisco].—Sato and Godinho, 1999:411, table 17.3 [Brazil, Rio São Francisco].—[Not Campos, 1945:450.]

Salmo corimbata Kner, 1859:146 [page 10 of separate], fig. 4a [type locality: Brazil, São Paulo, Varnhagen (= Ypanema), Rio Sorocaba basin].

Prochilodus oligolepis Günther, 1864:295 [type locality: Brazil, restricted herein to Brazil, São Paulo, Ipanema (Varnhagen), Rio Sorocaba basin; based upon specimens collected by Natterer that were cited as *Prochilodus nigricans* by Kner, 1859, but not conspecific with *Prochilodus nigricans* of Agassiz, 1829].—Steindachner, 1881:133 [redescription of species based upon Natterer specimens].—Eigenmann and Eigenmann, 1891:48 [in listing of South American fishes].—Eigenmann, 1907b:768 [lateral-line scale count]; 1910:424 [in listing of South American fishes].

(?) *Prochilodus hartii.*—Steindachner, 1874:533 [in part; Brazil, Rio Parahyba (= Paraíba)].—Fowler, 1975:359 [literature compilation; in part, only citation of occurrence of species in Rio Parahyba (= Paraíba), Brazil].

Prochilodus steindachneri Fowler, 1906:309, fig. 11 [type locality: Parahyba (= Paraíba), Brazil), restricted herein to Brazil, Rio de Janeiro, Rio Paraíba do Sul; *Chilomyzon* Fowler proposed as subgenus of *Prochilodus* with *P. steindachneri* as type species]; 1911:497 [comparison with *Prochilodus stigmaturus*]; 1950:224 [literature compilation, in part; not cited occurrence of species in states of Ceará and Pernambuco, Brazil]; 1975:360 [literature compilation].—Eigenmann, 1910:424 [in listing of South American fishes].—Ahl, 1937:136 [noted that *Prochilodus steindachneri* Fowler, 1906, had priority over *Prochilodus steindachneri* Eigenmann, 1922].—Mago-Leccia, 1972:47 [use of caudal-fin pigmentation to distinguish species groups].—Géry, 1977:219 [(Brazil), Rio Parahyba (= Paraíba); as possible synonym of *P. vimboides*].—Böhlke, 1984:148 [holotype depository; as possible senior synonym of *P. steindachneri*].—[Not Fowler, 1941:171.]

Prochilodus corimbata.—Fowler, 1906:311 [cited as closely related to *Prochilodus steindachneri*]; 1950:217 [literature compilation, in part; not cited occurrence of species in states of Ceará and Rio Grande do Norte, Brazil]; 1975:358 [literature compilation].—Géry, 1972b:33 [compared with *Curimatus* (= *Prochilodus*) *tigris*]; 1977:218 [in part; not synonymy of *P. cearensis*].—Mago-Leccia, 1972:47 [use of caudal-fin pigmentation to distinguish species groups].

DIAGNOSIS.—*Prochilodus vimboides* differs from all other species of *Prochilodus* in the number of scales along the lateral line (34 to 39 versus range of 40 to 64 in all other congeners in combination). *Prochilodus vimboides* further differs from *P. brevis, P. lacustris, P. mariae, P. nigricans,* and *P. rubrotaeniatus* in having hyaline caudal-fin lobes rather than dark, irregular, wavy bar-like patterns on the caudal-fin lobes. *Prochilodus vimboides* can be further discriminated from the seven species of *Prochilodus* with which it shares hyaline caudal fins (*P. argenteus, P. britskii, P. costatus, P. hartii, P. lineatus, P. magdalenae, P. reticulatus*) by the number of vertebrae (36 to 39 versus 40 or greater in the group consisting of *P. argenteus, P. britskii, P. costatus, P. lineatus*), the number of horizontal rows of scales around the caudal peduncle (13 to 15 versus 16 to 22 in the group consisting of *P. argenteus, P. costatus, P. lineatus, P. magdalenae, P. reticulatus*), and the number of horizontal rows of scales between the dorsal-fin origin and the lateral line (5 to 7 versus 8 to 11 in the group consisting of *P. argenteus, P. costatus, P. magdalenae*).

DESCRIPTION.—Morphometric and meristic data for *Prochilodus vimboides* presented in Table 17. Body comparatively high, transversely compressed. Greatest body depth at dorsal-fin origin. Dorsal profile of head gently convex. Predorsal profile of body convex. Body posteroventrally inclined along dorsal-fin base; gently convex from posterior of dorsal-fin base to adipose-fin origin and concave along caudal peduncle. Predorsal portion of body with slight median ridge. Postdorsal portion of body obtusely rounded transversely. Ventral profile of body convex from tip of lower jaw to posterior of anal fin, concave along caudal peduncle. Prepelvic region transversely flattened proximate to pelvic-fin insertion. Distinct median keel present between pelvic-fin insertion and anus.

TABLE 17.—Morphometrics and meristics of *Prochilodus vimboides:* (A) lectotype of *Prochilodus vimboides,* NMW 79466 (specimen dried and stuffed with straw); (B) paralectotypes of *Prochilodus vimboides,* NMW 79464–65 (specimens dried and stuffed with straw); (C) lectotype of *Prochilodus oligolepis,* NMW 56694; (D) paralectotypes of *Prochilodus oligolepis,* NMW 56693, NMW 56695:1–2; (E) holotype of *Prochilodus steindachneri,* ANSP 8207; and (F) all specimens of *Prochilodus vimboides* from which counts and measurements were taken (morphometric data for lectotype and paralectotypes of *P. vimboides* excluded from ranges as a consequence of method of preservation of those specimens; see "Remarks"). Standard length is presented in mm; values 2 to 16 are percentages of SL, 17 to 21 are percentages of HL. Dash indicates missing datum, and question mark indicates specimen damaged for the indicated feature.

Characters	A	B	C	D	E	F
			Morphometrics			
1. Standard length	179.4	176.1–176.6	139.5	134.6–137.4	97.5	57.7–328.6
2. Greatest body depth	30.8	30.1–31.2	36.8	33.8–37.7	39.6	30.1–43.1
3. Predorsal length	45.7	45.5–45.5	45.5	45.2–47.0	49.8	42.4–51.3
4. Dorsal-fin base length	14.4	12.8–15.0	15.6	14.6–15.7	17.5	14.6–18.0
5. Dorsal fin to adipose fin distance	30.4	30.9–31.0	27.7	27.7–30.5	27.2	23.9–31.5
6. Dorsal fin to caudal fin distance	45.9	44.9–45.1	43.8	44.3–48.0	41.1	39.3–50.0
7. Prepelvic length	52.2	51.3–52.2	53.5	52.0–54.2	57.1	49.9–57.2
8. Preanal distance	77.9	76.4–76.7	78.6	77.4–78.9	78.1	72.1–82.1
9. Snout to anal-fin insertion	80.4	80.0–81.2	80.9	79.9–81.6	80.1	76.8–83.8
10. Anal-fin base length	9.6	9.5–10.1	9.3	8.5–10.3	10.3	8.2–15.0
11. Caudal-peduncle length	13.7	13.7–13.7	14.6	13.6–14.8	12.4	10.3–14.8
12. Dorsal-fin length	20.0?	17.0–17.7?	25.4	25.0–26.5	28.7	23.6–34.9
13. Pectoral-fin length	18.3	15.0–16.9	20.5	18.7–20.1	20.7	17.4–23.1
14. Pelvic-fin length	15.9?	11.7–12.2?	16.8	16.8–17.7	19.4	16.3–22.4
15. Least caudal-peduncle height	11.7	9.5–9.5	12.3	11.4–12.2	11.6	10.3–13.7
16. Head length	23.2	22.8–23.4	24.5	24.5–24.7	28.2	21.9–31.4
17. Snout length	36.8	37.9–38.2	36.8	36.1–38.7	36.0	29.9–46.4
18. Bony orbital diameter	24.3	21.8–22.8	22.8	22.6–25.9	27.6	16.6–34.5
19. Postorbital length	43.0	42.4–44.2	43.6	43.1–45.2	38.5	31.8–46.3
20. Interorbital width	47.1	48.6–48.7	49.1	49.0–49.7	49.5	46.1–54.0
21. Mouth width	–	–	42.1	38.3–43.1	42.2	35.5–46.1
			Meristics			
Lateral-line scales	36	35–36	37	36–37	36	34–39
Scale rows between dorsal-fin origin and lateral line	6	6	6	6	7	5–7
Scale rows between anal-fin origin and lateral line	5	5	5	5	6	4–6
Scale rows between pelvic-fin insertion and lateral line	6	6	6	6	6	5–7
Rows of scales around caudal peduncle	14	14	14	14	14	13–15
Median predorsal scales	13	12–13	14	12–13	13	11–16
Median scales between dorsal and adipose fins	13	13	13	13–14	13	11–15
Vertebrae	–	–	37	37–38	38	36–39
Inner row teeth, upper jaw	–	–	12	11–12	14	11–21
Inner row teeth, lower jaw	–	–	6	6–8	9	6–13

Head profile pointed. Mouth terminal. Snout length greater than horizontal width of orbit. Nares of each side of head close to each other; anterior nares circular, posterior nares crescent shaped. Adipose eyelid present but poorly developed; most developed anteriorly, but with greater part of eye uncovered. Lips fleshy, moderately developed relative to those in some other prochilodontids, and forming oral disk when protracted.

Functional teeth in two rows in each jaw. All teeth movably implanted in flesh that overlies jaws. All teeth of similar size, with exposed portion spoon shaped except when worn down. Inner tooth series in each jaw with 11 to 21 teeth on left side of upper jaw and 6 to 13 teeth on left side of lower jaw. Outer row of teeth in each jaw with approximately 45 teeth on each side of upper jaw and approximately 42 teeth on each side of lower jaw in lectotype. Upper and lower lips bordered by numerous globular, fleshy papillae.

Scales spinoid. Scales in middorsal series between posterior of dorsal-fin base and adipose-fin origin similar in form to those of adjoining regions of body. Lateral line with 34 to 39 (44.8% of specimens with 37) scales; 5 to 7 (86.6% of specimens with 6) horizontal rows of scales between dorsal-fin origin and lateral line; 5 to 7 (80.6% of specimens with 6) horizontal rows of scales between pelvic-fin insertion and lateral line; 4 to 6 (77.6% of specimens with 5) horizontal rows of scales between anal-fin origin and lateral line; 11 to 16 (43.3% of specimens with 13) median predorsal scales; 11 to 15 (38.8% of specimens with 12) scales in middorsal series between posterior of dorsal-fin base and adipose-fin origin; 13 to

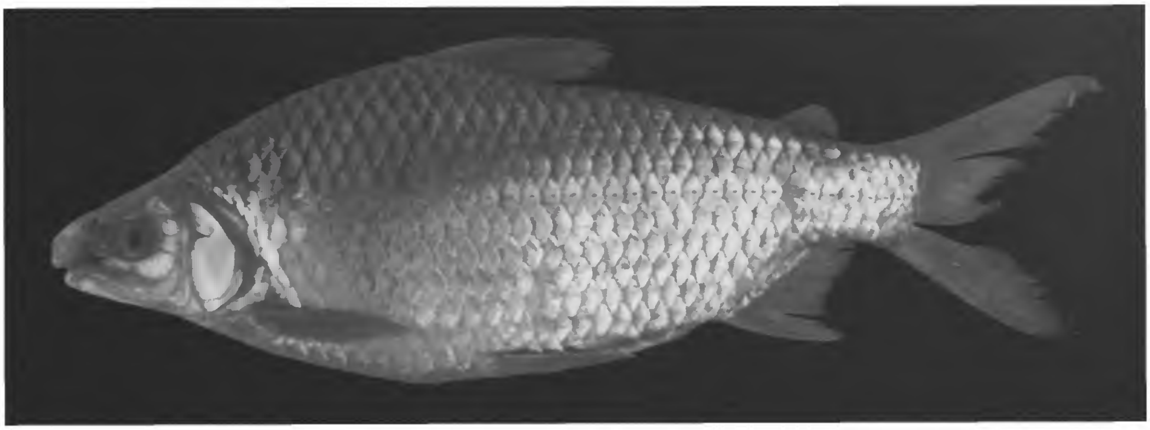


FIGURE 59.—*Prochilodus vimboides*, NMW 56716:1, 274.6 mm SL; Brazil, Espirito Santo or Minas Gerais, Rio Doce.

15 (89.6% of specimens with 14) horizontal rows of scales around caudal peduncle.

Dorsal fin preceded by small, but well-developed, anteroventrally bifurcate, procumbent spine somewhat triangular in lateral view. Dorsal-fin rays (including procumbent spine) iii,9 or 10 (iii,10 most frequent) [iii,10]; anal-fin rays iii,7 to 9, or ii,8 (iii,8 most frequent) [iii,8]; pectoral-fin rays i,12 to 15 (i,14 most frequent) [?]; pelvic-fin rays i,8 or 9 (i,8 most frequent) [i,8]; principal caudal-fin rays 10/9 [10/9].

Vertebrae 36 to 39 (40.9% of specimens with 38).

Dorsal fin truncate, slightly pointed distally; posterior unbranched rays and anterior branched rays longest and subequal. Dorsal-fin origin located closer to tip of snout than to caudal-fin base. Greatest length of adipose fin approximately equal to horizontal width of orbit. Adipose-fin origin located along vertical that passes through middle of anal-fin base. Pectoral fin distally pointed. Tip of adpressed pectoral fin reaching approximately two-thirds of distance between pectoral-fin and pelvic-fin insertions. Pelvic fin falcate. Pelvic-fin insertion located slightly posterior to vertical that passes through anterior one-third of dorsal-fin base. Tip of adpressed pelvic fin reaching posteriorly approximately three-fourths of distance between pelvic-fin insertion and anus. Axillary scale present, its length approximately one-third of greatest length of pelvic fin. Posterior unbranched and anterior branched anal-fin rays longest and subequal. Caudal fin bifurcate.

COLORATION IN ALCOHOL.—Ground coloration silvery yellow, with dorsal portions of body and head darker. Lateral surface of body with 6 to 15 dark, vertically elongate, diffuse and irregular patches of pigmentation between head and caudal fin. Patches with approximate overall form of narrow isosceles triangles, with apexes located along middle of ventrolateral portion of body and bases on dorsomedial region of body. Patches well developed in small specimens, but indistinct or absent in large individuals. Lateral surface of body lacking distinct, dark, wavy, horizontal stripes present in many congeneric species. Faint field of black or brown chromatophores forming patch of irregular dark pigmentation on upper one-half of opercle and on lateral exposed portion of pectoral girdle.

Dorsal fin with 3 to 8 (most frequently 5) dark, irregular stripes beginning at anterior margin and extending across fin approximately parallel to base of fin. Adipose fin with dorsal margin somewhat dusky. Pectoral, pelvic, anal, and caudal fins hyaline to slightly dusky. Iris yellowish silver, with diffuse dusky areas on dorsal and ventral portions.

COLORATION IN LIFE.—(based upon color transparencies of recently collected specimens from the Rio Jucurucu basin, Bahia, taken by the first author and from the Rio Doce system, Espírito Santo taken by Flavio A. Bockmann, LIRP). Ground coloration of head and body silvery. Dorsal portions of head and particularly body much darker. Dorsal fin dusky hyaline. Pectoral fin hyaline or slightly yellowish to reddish yellow. Pelvic fin with anterior region milky white and remaining portion reddish orange. Interradial membranes of anal and caudal fins dusky, with posterior margins bright red; width of marginal red pigmentation approximately equal to horizontal width of pupil. Iris golden yellow.

DISTRIBUTION.—*Prochilodus vimboides* is known from the coastal rivers of Brazil through the region from the Rio Jequitinhonha in the states of Bahia and Minas Gerais to the Rio Paraíba do Sul in the state of Rio de Janeiro, the rivers of the eastern portions of the upper Rio Paraná basin in Brazil, and the Rio São Francisco near Três Marias (Figure 52, squares).

COMMON NAME.—Grumexa, grumecha, corimbatá, curimbatá, corimbatá-de-lagoa (Brazil).

COMPARISONS.—As noted in the "Diagnosis," above, *Prochilodus vimboides* is readily distinguishable from all of its congeners on the basis of a series of meristic and/or pigmentary features.

REMARKS.—The description of *Prochilodus vimboides* (Kner, 1859:12–13, pl. 2: fig. 4a) was based upon material collected by Natterer at Ypanema (=Varnhagen), São Paulo, Brazil. The three known syntypes of *P. vimboides* in the Naturhistorisches Museum Wien (NMW) are dried and presumably mostly defleshed specimens that are stuffed with straw. We herein designate NMW 79466 (179.4 mm SL), the specimen in the best overall condition, as the lectotype of the species, and the other two syntypes (NMW 79464, 176.1 mm SL; NMW 79465, 176.6 mm SL) consequently become paralectotypes.

In a brief account, Kner (1859:146) identified four specimens collected by Natterer in Ypanema (=Varnhagen), São Paulo, Brazil, as *Prochilodus nigricans* and mentioned in passing that Natterer had identified this species in a manuscript as *Salmo corimbata,* thereby making the latter name available.

In his original description of *P. vimboides* (1859:149), Kner remarked that the species is very similar to specimens that he identified as *P. nigricans* in the same publication (1859:146). He differentiated the two samples on the basis of scale form, with the material of *P. vimboides* (NMW 79464, 79465, 79466) cited as having smooth exposed margins, whereas the specimens that he identified as *P. nigricans* (NMW 56693, 56694, 56695) were reported to have irregular scale margins. Comparisons of the two series of specimens reported on by Kner (1859) as different species failed to reveal any difference in the margins of the scales between the two purported forms, even in instances where the varnish layer, which mostly overlies the scales, had fallen off in the dried and stuffed specimens, thereby facilitating direct comparisons of the details of the scales in the two samples.

Soon thereafter, Günther (1864:295), in a very brief description, proposed a new species, *Prochilodus oligolepis.* The description of this new species was based upon the specimens from Ypanema (=Ipanema) that had been identified by Kner (1859:146) as *P. nigricans.* There is, however, no indication that Günther examined the material reported on by Kner. In his description of *P. oligolepis,* Günther focused on the different numbers of lateral-line scales in *P. nigricans* and *P. oligolepis.* Presumably, Günther was influenced by Kner's identification of his material from Ipanema as *P. nigricans,* but Günther did not discuss any feature that might distinguish *P. oligolepis* from *P. vimboides.* Although *P. vimboides* does indeed differ from *P. nigricans* in a number of features, including the lateral-line scale count originally cited by Günther (1864), an examination of the syntype series of *P. oligolepis* and *P. vimboides* has failed to reveal any differences between those nominal forms (Table 17). *Prochilodus oligolepis* is consequently considered to be a junior synonym of *P. vimboides.* We herein designate NMW 56694 (139.5 mm SL), the syntype in the best condition, as the lectotype of *P. oligolepis*, and the three remaining known syntypes of the species (NMW 56693, NMW 56695:1, NMW 56695:2) consequently become paralectotypes.

Fowler's (1906:309–311, fig. 11) description of *Prochilodus steindachneri* was based upon a specimen with a stated locality of "Parahyba, Brazil," which had originally been deposited in the Museum of Comparative Zoology (MCZ). The holotype of *P. steindachneri* was, however, collected by the Thayer Expedition in the Rio Paraíba do Sul of southeastern Brazil, rather than in the state of Paraíba in northeastern Brazil. This misinterpretation lead to *P. steindachneri* being erroneously cited as a component of the ichthyofauna of northeastern Brazil in various publications by Fowler and subsequent authors. No differences have been found in this study to discriminate *P. steindachneri* from *P. vimboides* (Table 17), and *P. steindachneri* is consequently considered to be a junior synonym of *P. vimboides.* The only *Prochilodus* species known to occur in the state of Paraíba, Brazil, is *P. brevis,* and citations of *P. steindachneri* from the state of Paraíba most likely refer to *P. brevis.*

In the publication in which he described *Prochilodus steindachneri,* Fowler (1906:311) also called attention to the priority of *Salmo corimbata,* a manuscript name made available by Kner (1859:146), over *Prochilodus oligolepis* Günther, 1864. Fowler (1950, 1975) continued to utilize the combination *Prochilodus corimbata* as the senior synonym of *P. oligolepis,* a practice followed by a few other authors. Because of the fact that *P. vimboides* and *P. corimbata* were published in the same publication and refer to the same species, the two names have equivalent status in terms of priority. Under the principle of first revisors (article 24.2 of the International Code of Zoological Nomenclature), and in order to maintain stability in the nomenclature of the group, we establish herein the priority of *Prochilodus vimboides* Kner, 1859, over *Prochilodus corimbata* (Kner, 1859), making the latter species a junior synonym of the former.

Prochilodus vimboides is unknown from the small to medium-size coastal rivers of Brazil located north of the Rio Jucurucu, Bahia. Citation of that species or its synonyms from the rivers basins in that region refer to either to *P. brevis* or *P. hartii,* both of which occur in the drainages of that area. In many instances, it is impossible to determine which of these species was the basis for a specific literature record.

No differences were found in this study between the populations of *Prochilodus vimboides* from the shorter coastal rivers of eastern Brazil, the upper portion of the Rio Paraná (upriver of the rapids of Salto de Sete Quedas that are now inundated by the Itaipu Reservoir (Reis et al., 1992:271)), and those from the Rio São Francisco. These populations are consequently considered to be conspecific despite this unusual distribution for a prochilodontid species, straddling as it does the divides between the upper courses of several drainage systems.

One examined specimen of *Prochilodus vimboides* (MZUSP 3800) has a stated locality of "Rio São Francisco, Bahia," which is considerably to the north of the known limits of distribution of *P. vimboides.* The locality information associated with this specimen is, however, questionable (Heraldo A. Britski, MZUSP, pers. comm., 2002) and no other specimens of the species are known from that region. We consequently consider this record to be erroneous.

A second specimen of *Prochilodus vimboides* (MZUSP 1688) has a purported collection locality of Brazil, Rio Grande do Sul, Itaqui, a site in the Rio Uruguay basin that lies distinctly outside the known range of *P. vimboides*. Questions exist about the locality information associated with some of the older collections in the MZUSP holdings (Heraldo A. Britski, MZUSP, pers. comm. 2002), and this lot of *P. vimboides* was part of a shipment sent to CAS in 1930 for identification (information from CAS archives). Locality information associated with at least some of the material in that shipment was apparently transposed at some point during the processing and identification of the specimens, resulting in a number of questionable stated localities (Britski, 1969:200, 203). One lot particularly pertinent to the question at hand involves material of *Leporinus amblyrhynchus* in the MZUSP collections that also purportedly originated at Itaqui and that was included in that shipment to CAS. Garavello and Britski (1987:159) noted that this Itaqui record for *L. amblyrhynchus* lies distant from the known range of the species, and those authors suggested that this locality is erroneous. Given the pattern of problems with the locality information for material in that shipment sent to CAS and the lack of any other records of *P. vimboides* from the portions of the Rio Paraná basin below the location of the now inundated Sete Quedas falls, we consider the locality information of "Brazil, Rio Grande do Sul, Itaqui" associated with MZUSP 1688 to be erroneous.

A third *P. vimboides* specimen (USNM 26696) is indicated to have originated from "Brazil, Amazon." This specimen had been received on exchange from MCZ and was originally identified as "Curimatus parahybae," which apparently is an unpublished manuscript name. The specimen is comparable in size and condition to MCZ Thayer Expedition samples from the Rio Paraíba do Sul, state of Rio de Janeiro, Brazil. That location would account for the manuscript name of "parahybae" (Parahyba being the spelling of the name of the river associated with Thayer Expedition material, see Higuchi, 1996). Another lot of *P. vimboides* (USNM 1163761, formerly CU 1575) that had been originally at MCZ and that was first identified as "Curimatus parahybae" has an original locality of "Brazil: Parahyba"; thus, it seems likely that the locality information associated with USNM 26696 is erroneous.

MATERIAL EXAMINED.—257 specimens (62, 57.7–328.6 mm SL).

BRAZIL. *Bahia:* Santa Clara, Rio Mucuri, MCZ 20039, 6 (1, 199.4–240.7) [1R]; MCZ 20040, 3 (1, 180.5–229.6) [1R]; NMW 56719, 1 (1, 251.3); NMW 56722:1, 1 (1, 245.0). Mucuri (Porto Alegre), NMW 56722:2–3, 2 (1, 205.8). Rio Mucuri, approximately 6.6 km upriver of Mucuri (Porto Alegre), MCZ 20046, 5 (1, 198.7–218.3) [1R]. Rio Jucurucu, approximately 16 km from Itamaraju, MZUSP 42680, 3 (3, 166.9–193.3) [3R], MZUSP 42719, 1 (cleared and counterstained for bone and cartilage); USNM 319767, 2 (2, 180.9–186.7) [2R]. Rio Mucuri, upriver of Mucuri (Porto Alegre) and Santa Clara, NMW 56721, 2 (2, 219.8–245.2). *Espirito Santo:* Lagoa de Juparanã, Linhares, MZUSP 20783, 1 (1, 210.0); MZUSP 20856, 3 (3, 153.0–252.0). Rio São José das Torres, on highway BR-101, between Campos and Cachoeiro de Itapemirim, MZUSP 27572, 1 (1, 121.5). Rio do Frade e da Freira, Cachoeiro de Itapemirim, MZUSP 20849, 1 (1, 57.7). Colatina, Rio Doce, MZUSP 20854, 1 (1, 240). Rio Doce, near Linhares and Lagoa de Juparanã, MZUSP 2010, 4 (4, 61.7–130.0). Rio Doce, between Linhares and Aimorés, MCZ 20033, 1 (1, 328.6). *Minas Gerais:* Lagoa Amarela, Rio Doce basin, MZUSP 36640, 6 (2, 223.4–230.5). Lago Jacaré, Rio Doce basin, MZUSP 36656, 6 (2, 185.8–231.7). Lagoa Jacaré, Rio Doce, MZUSP 2859, 1 (1, 194.0). Município de Joanésia, Rio Santo Antonio, Rio Doce basin, LIRP 274, 1. Lagoa da Prata, Rio São Francisco, MZUSP 28317, 1 (71.0). Riacho tributary to Rio Jequitaí, along highway BR-135, between Buenópolis and Engenheiro Dolabela (latter locality at 17°30′S, 44°05′W), USNM 345752, 3 (82.0–128.8). Rio Mucuri, approximately 9 km W of Presidente Pena, Fazenda Gavião (Presidente Pena at 17°41′S, 40°55′W), USNM 318138, 3 (178.2–208.4); USNM 318169, 3 (191.9–287.0). Lago Don Helvécio, Rio Doce basin, MZUSP 36666, 1 (1, 302.1). Teófilo Otoni, MZUSP 1678, 1 (1, 123.3). *Rio de Janeiro:* Rio Paraíba (do Sul), ANSP 8207, 1 (1, 97.5, holotype of *Prochilodus steindachneri*) [1R]; MCZ 20167, 2 (1, 177.0) [1R]; MCZ 20168, 55 (70.2–127.1); MCZ 20169, 38 (85.2–128.0); MCZ 20170, 4 (81.6–110.0); MCZ 20351, 22 (75.1–173.1). Porto Real, BMNH 1891.6.16:58–9, 2 (1, 208.5–234.9) [2R]. Rio Paraíba (do Sul), Entre Rios, FMNH 76364 (formerly CM 4419), 1 (184.2). Rio Muriaé, in Muriaé, MCZ 20036, 2 (1, 230.4–238.1) [1R]. Rio Muriaé, Cardoso Moreira, MZUSP 20665, 1 (1, 96.4). Mendes, MCZ 20037, 6 (1, 117.2–143.4) [1R]; MCZ 20038, 1 (241.1); NMW 56721, 17 (2, 81.7–82.7). Lagoa Feia, MZUSP 1541, 1 (1, 242.0). MZUSP 2047, 1 (1, 225.0). Rio Paraíba (do Sul), near Rio de Janeiro, MCZ 20166, 1 (1, 222.1) [1R]. Campos, MCZ 20041, 2 (108.7–123.5). *São Paulo:* Varnhagen (=Ipanema), Rio Sorocaba basin NMW 56693, 1 (1, 137.4, paralectotype of *Prochilodus oligolepis*) [1R]; NMW 56694, 1 (1, 139.5, lectotype of *Prochilodus oligolepis*) [1R]; NMW 56695:1, 1 (1, 134.6, paralectotype of *Prochilodus oligolepis*) [1R]; NMW 56695:2, 1 (1, 137.0, paralectotype of *Prochilodus oligolepis*) [1R]; NMW 79464, 1 (1, 176.1, paralectotype of *Prochilodus vimboides*); NMW 79465, 1 (1, 176.6, paralectotype of *Prochilodus vimboides*); NMW 79466, 1 (1, 179.4, lectotype of *Prochilodus vimboides*). Emas, Pirassununga, MZUSP 20669, 1 (1, 205.6). Rio Mogi-Guaçu, Pirassununga, MZUSP 2058, 1 (1, 155.8). Emas, Rio Mogi-Guaçu, MZUSP 3434, 1 (1, 218.5). Piracicaba, MZUSP 1775, 1 (1, 125.2). Taubaté, MZUSP 1784, 3 (1, 99.7–132.9). Rio Aguapeí, MZUSP 3047, 1 (1, 109.3). Piracicaba or Pirassununga, CAS 11829 (formerly MZUSP 2799), 1 (97.2); CAS 11902 (formerly MZUSP 1427), 1 (234.7). State of São Paulo, MZUSP 214600, 2 (149.0–160.0). *Inexact Locality:* Rio

Grande, MNHN 09.203, 1 (1, 179.0); MNHN 09.204, 1 (1, 204.5); NMW 56723, 1 (178.6). Rio Doce, FMNH 78088, 1 (1, 22.6) [1R]; NMW 56716, 13 (3, 255.9–274.6) [1R]. Rio Doce, Fumaça, 2 mi (=3.2 km) upriver of Vila Rio Doce, FMNH 92303, 1 (1, 167.7) [1R].

QUESTIONABLE LOCALITIES.—BRAZIL. "Amazon," USNM 26696, 1 (76.8; see under "Remarks," above, concerning this locality). *Bahia:* Rio São Francisco, MZUSP 3800, 1 (156.1; see under "Remarks," above, concerning this locality). *Rio Grande do Sul:* Itaqui, MZUSP 1688, 1 (116.2; see under "Remarks," above, concerning this locality).

Genus *Semaprochilodus* Fowler, 1941

Semaprochilodus Fowler, 1941:171 [type species: *Prochilodus squamilentus* Fowler, 1941 (type species cited as *Semaprochilodus squamilentus* in accompanying species description (Fowler, 1941:172)) by original designation and monotypy (=*Semaprochilodus brama* (Valenciennes, 1850))]. Gender masculine.

DIAGNOSIS.—*Semaprochilodus* is a monophyletic group delimited by the characters discussed under "Monophyly of *Semaprochilodus,*" above. The genus can be differentiated from *Ichthyoelephas* and *Prochilodus,* the two other genera of the Prochilodontidae, by the following combination of characters: the dorsal fin is preceded by an anteriorly bifurcate procumbent spine; the fleshy lips are less developed than in *Ichthyoelephas* and *Prochilodus,* albeit much more pronounced than the lips in other characiforms; the teeth are short and spoon shaped in frontal view; there are 7 to 16 teeth in the inner tooth row on each side of the upper jaw and 4 to 11 teeth on the inner tooth row of the lower jaw; the scales are cycloid, with smooth borders and membranous margins; the scales in the middorsal series between the posterior of the dorsal-fin base and the adipose-fin origin have a relatively well-developed spatulate process along the posterior margin of each scale in that series; the dorsal fin is distally pointed, with 2 to 5 dark, irregular stripes beginning along the anterior of the dorsal-fin margin and extending across the fin approximately parallel to the fin base; the anal fin is falcate, with up to 5 oblique, irregular, dark stripes; the caudal fin is moderately bifurcate, with a total of 5 to 15 dark stripes composed of a horizontal stripe extending along the middle caudal-fin rays and 2 to 7 oblique stripes on each lobe of the caudal fin; and the membranous border of the opercle and lateral exposed portion of pectoral girdle are darkly pigmented to different degrees of duskiness.

In addition, *Semaprochilodus* has 39 to 77 pored scales along the lateral line; 8 to 14 horizontal rows of scales between the dorsal-fin origin and the lateral line; 7 to 14 horizontal rows of scales from the pelvic-fin insertion to the lateral line; 6 to 12 horizontal rows of scales between the anal-fin origin and the lateral line; 10 to 22 median predorsal scales; 11 to 26 scales in the middorsal series between the posterior of the dorsal-fin base and the adipose-fin origin; 16 to 27 horizontal rows of scales around the caudal peduncle; and 35 to 43 vertebrae.

Semaprochilodus includes six species according to the results of this study, with the members of the genus being limited to the Rio Amazonas, Río Orinoco, and Marowijne River-Fleuve Maroni basins; this is a significantly more restricted geographic distribution than that of the family as a whole. Interspecific variation within *Semaprochilodus,* albeit moderate, is more pronounced than in the other genera in the Prochilodontidae, with the maximum known lengths of the included species ranging from approximately 238 to 438 mm SL.

REMARKS.—Species assigned in this study to *Semaprochilodus* were originally described in, or subsequently assigned to, diverse genera. The first of these species to be described was *Curimatus taeniurus* Valenciennes, 1817. Müller and Troschel (1844) subsequently used the combination *Anodus taeniurus* for that species; however, *Anodus* Cuvier has as its type *Anodus elongatus* Agassiz, a component of the Hemiodontidae (Langeani, 1998), and *Anodus* is unavailable in the Prochilodontidae. Kner (1859), in turn, described a species, *Salmo jaraqui,* that we find to be equivalent to *Semaprochilodus insignis,* which was originally described by Jardine (1841) as *Prochilodus insignis.* The type species of *Salmo,* however, does not belong to the Prochilodontidae; rather, it is a member of the family Salmonidae, a group distant phylogenetically from the order Characiforms that includes the Prochilodontidae.

The other nominal species now assigned to *Semaprochilodus* were all originally described in *Prochilodus* until Fowler (1941) proposed the new genus, with *Prochilodus squamilentus* as its type species. That species is, however, a junior synonym of *Semaprochilodus brama* (Valenciennes, 1850). Nonetheless, authors following Fowler (1941), most notably Mago-Leccia (1972), brought together within *Semaprochilodus* various species that had been previously included in other prochilodontid genera, a practice validated by the results of this study. As noted under the "Phylogenetic Reconstruction," above, *Semaprochilodus* is defined by a series of internal synapomorphies in addition to being readily recognizable on the basis of various distinctive external features, most of which are derived.

Key to the Species of *Semaprochilodus*

1. Membranous opercular border and exposed surface of the pectoral girdle weakly pigmented with black; 39 to 43 vertebrae (Río Orinoco, Rio Amazonas basin) 2
   Membranous opercular border and exposed surface of the pectoral girdle intensely pigmented with black; 35 to 37 vertebrae (Río Orinoco, Rio Tocantins, Rio Xingu, and Marowijne River-Fleuve Maroni system) 4

2. Scales in lateral line 64 to 77; 12 to 14 horizontal rows of scales between dorsal-fin origin and lateral line; 12 to 14 horizontal rows of scales between pelvic-fin insertion and lateral line; 23 to 26 horizontal rows of scales around caudal peduncle .... ***S. taeniurus*** (Amazon basin)

Scales in lateral line 45 to 53; 8 to 11 horizontal rows of scales between dorsal-fin origin and lateral line; 7 to 11 horizontal rows of scales between pelvic-fin insertion and lateral line; 16 to 22 horizontal rows of scales around caudal peduncle (Río Orinoco and Rio Amazonas basins) 3

3. Horizontal rows of scales between dorsal-fin origin and lateral line 8 or 9 (8 most frequent) [Figure 64]; 7 to 9 horizontal rows of scales from pelvic-fin insertion to lateral line (8 most frequent) [Figure 65]; 6 or 7 horizontal rows of scales from anal-fin origin to lateral line (6 most frequent) [Figure 63]; lateral line with 45 to 49 scales (47 most frequent) [Figure 66] .... ***S. kneri*** (Río Orinoco basin)

Horizontal rows of scales between dorsal-fin origin and lateral line 9 to 11 (10 most frequent) [Figure 64]; 9 to 11 horizontal rows of scales between pelvic-fin insertion and lateral line (10 most frequent) [Figure 65]; 7 to 9 horizontal rows of scales between anal-fin origin and lateral line (8 most frequent) [Figure 63]; lateral line with 47 to 53 scales (48 most frequent) [Figure 66] .... ***S. insignis*** (Amazon basin)

4. Lateral line with 39 to 41 scales; 8 horizontal rows of scales between dorsal-fin origin and lateral line; 16 horizontal rows of scales around caudal peduncle ..... ***S. varii*** (Marowijne River-Fleuve Maroni basin, Suriname and French Guiana)

Lateral line with 48 to 68 scales; 10 to 13 horizontal rows of scales between dorsal-fin origin and lateral line; 19 to 27 horizontal rows of scales around caudal peduncle (Río Orinoco, Rios Tocantins and Xingu) 5

5. Horizontal rows of scales between anal-fin origin and lateral line 8 or 9; lateral line with 48 to 56 scales (51 most frequent); 19 to 24 horizontal rows of scales around caudal peduncle (22 most frequent) .... ***S. laticeps*** (Río Orinoco basin)

Horizontal rows of scales between anal-fin origin and lateral line 10 to 12; lateral line with 56 to 68 scales (58 most frequent); 23 to 27 horizontal rows of scales around caudal peduncle (24 most frequent) .... ***S. brama*** (Rio Tocantins and Rio Xingú basins)

Chave de Identificação das Espécies de *Semaprochilodus*

1. Borda opercular membranosa e superfície lateral exposta da cintura peitoral fracamente pigmentadas de negro; 39–43 vértebras (bacias dos Rios Orinoco e Amazonas) . . . 2

Borda opercular membranosa e superfície lateral exposta da cintura peitoral intensamente pigmentadas de negro; 35–37 vértebras (bacias dos Rios Orinoco, Marowijne, Tocantins e Xingu).. 4

2. Escamas na linha lateral 64–77; 12–14 fileiras transversais de escamas da origem da nadadeira dorsal à linha lateral; 12–14 fileiras horizontais de escamas da origem da nadadeira pélvica à linha lateral; 23–26 fileiras horizontais de escamas em torno do pedúnculo caudal .... ***S. taeniurus*** (bacia Amazônica)

Escamas na linha lateral 45–53; 8–11 fileiras transversais de escamas da origem da nadadeira dorsal à linha lateral; 7–11 fileiras horizontais de escamas da origem da nadadeira pélvica à linha lateral;16–22 fileiras horizontais de escamas em torno do pedúnculo caudal (bacias do Río Orinoco e Rio Amazônica)................ 3

3. Fileiras transversais de escamas da origem da nadadeira dorsal à linha lateral 8–9 (8 mais frequente) [Figura 64]; 7–9 fileiras horizontais de escamas da origem da nadeira pélvica à linha lateral (8 mais frequente) [Figura 65]; 6–7 fileiras horizontais de escamas da origem da nadadeira anal à linha lateral (6 mais frequente) [Figura 63]; linha lateral com 45–49 escamas (47 mais frequente) [Figura 66] .... ***S. kneri***
(bacia do Río Orinoco)

Fileiras transversais de escamas da origem da nadadeira dorsal à linha lateral 9–11 (10 mais frequente) [Figura 64]; 9–11 fileiras horizontais de escamas da origem da nadadeira pélvica à linha lateral (10 mais frequente) [Figura 65]; 7–9 fileiras horizontais de escamas da origem da nadeira anal à linha lateral (8 mais frequente) [Figura 63]; linha lateral com 47–53 escamas (48 mais frequente) [Figura 66] .... ***S. insignis***
(bacia Amazônica)

4. Linha lateral com 39–41 escamas; 8 fileiras transversais de escamas da origem da nadadeira dorsal à linha lateral; 16 fileiras horizontais de escamas em torno do pedúnculo caudal .... ***S. varii***
(bacia do Rio Marowijne,
Suriname e Guiana Francesca)

Linha lateral com 48–68 escamas; 10–13 fileiras transversais de escamas da origem da nadadeira dorsal à linha lateral; 19–27 fileiras horizontais de escamas em torno do pedúnculo caudal (bacias dos Rios Orinoco, Tocantins e Xingú) 5

5. Fileiras horizontais de escamas da origem da nadadeira anal à linha lateral 8–9; 19–24 fileiras horizontais de escamas em torno do pedúnculo caudal (22 mais frequente); linha lateral com 48–56 escamas (51 mais frequente) .... ***S. laticeps***
(bacia do Río Orinoco)

Fileiras horizontais de escamas da origem da nadadeira anal à linha lateral 10–12; 23–27 fileiras horizontais de escamas em torno do pedúnculo caudal (24 mais frequente); linha lateral com 56–68 escamas (58 mais frequente) .... ***S. brama***
(bacias dos Rios Tocantins e Xingú)

Semaprochilodus brama (Valenciennes, 1850)

FIGURES 60, 61; TABLE 18

Prochilodus brama Valenciennes in Cuvier and Valenciennes, 1850:82 [type locality: l'Amazone (= Rio Amazonas), restricted herein to Brazil, Pará, Rio Tocantins, São João do Araguaia (São João das Duas Barras)].—Castelnau, 1855:62, pl. 31: fig. 2 [redescription based upon holotype].—Günther, 1864: 296 [based upon Valenciennes, 1850].—Eigenmann and Eigenmann, 1891: 48 [in listing of South American fishes].—Ulrey, 1895:259 [Brazil, Rio Tocantins, Trocera].—Gill, 1896:209 [details of skull anatomy].—Eigenmann, 1910:424 [in part, Amazon basin, not citation of species for Río Orinoco basin].—Bertin, 1947:35 [holotype depository].—Fowler, 1950:216 [literature compilation]; 1975:358 [literature compilation].—Géry, 1964b:467 [Brazil, upper Rio Araguaia]; 1977:219 [as very close to *Prochilodus mariae*].—Mago-Leccia, 1972:47 [use of caudal-fin pigmentation to distinguish species groups].—[Not Peters, 1877:477 [purported occurrence of species in Río Orinoco basin].]

Semaprochilodus squamilentus Fowler, 1941:172, fig. 83 [type locality: Rio Parnahyba, Therezina, Piauhy, eastern Brazil (=Rio Parnaíba, Terezina, Piauí, Brazil), corrected herein to Brazil, Rios Tocantins and/or Xingu]; 1950: 227 [literature compilation]; 1975:361 [literature compilation].—Mago-Leccia, 1972:58 [as species of *Semaprochilodus*].—Roberts, 1973b:213 [originally reported type locality questioned].—Géry, 1977:218 [eastern Brazil].—Böhlke, 1984:148 [holotype and paratype depository; problematic type locality noted].—Mérona, 1987:120 [Brazil, lower Rio Tocantins; ecology].—Castro, 1988:504 [comparison with *Semaprochilodus varii*].

Prochilodus squamilentus.—Fowler, 1941:171 [cited as type species of genus *Semaprochilodus* proposed on same page, apparent error].—Böhlke, 1984: 148 [erroneous use of *Prochilodus* rather than *Semaprochilodus* by Fowler (1941) noted].

Semaprochilodus brama.—Santos et al., 1984:27 [Brazil, Rio Tocantins; commercial importance; life history].—Nomura, 1984:58 [Brazil, common name].—Mérona, 1987:120 [Brazil, lower Rio Tocantins; ecology].—Braga, 1990:549, table 1 [Brazil, Rio Tocantins; feeding and reproduction].—Menezes and Vazzoler, 1992:63 [reproductive characteristics].

DIAGNOSIS.—*Semaprochilodus brama* is distinguished from all congeners except *S. varii* and *S. laticeps* in having the membranous border of the opercle and the exposed portion of the pectoral girdle intensely pigmented with black. It can be readily distinguished from *S. varii* in the number of scales along the lateral line (56 to 68 versus 39 to 41, respectively), the number of horizontal rows of scales between the dorsal-fin origin and the lateral line (11 to 13 versus 8, respectively), and the number of horizontal rows of scales around the caudal peduncle (23 to 27 versus 16, respectively); and from *S. laticeps* in the number of horizontal rows of scales between the anal-fin origin and lateral line (10 to 12 versus 8 or 9, respectively) and in the number of scales along the lateral line (56 to 68, 58 most frequent and 56 in only 4 of 26 specimens examined for this feature, versus 48 to 56, 51 most frequent and 56 in only 2 of 27 specimens examined for this feature, respectively).

DESCRIPTION.—Morphometric and meristic data for *Semaprochilodus brama* presented in Table 18. Body high and

TABLE 18.—Morphometrics and meristics of *Semaprochilodus brama:* (A) holotype of *Prochilodus brama,* MNHN A.1066 (specimen dried and stuffed with straw); (B) holotype of *Semaprochilodus squamilentus,* ANSP 69480; (C) paratype of *Semaprochilodus squamilentus,* ANSP 69481; and (D) all specimens of *Semaprochilodus brama* from which counts and measurements were taken (morphometric data for holotype of *Prochilodus brama* excluded from ranges as a consequence of method of preservation of that specimen; see "Remarks"). Standard length is presented in mm; values 2 to 16 are percentages of SL, 17 to 21 are percentages of HL. Dash indicates missing datum, and question mark indicates specimen damaged for the indicated feature.

Characters	A	B	C	D
		Morphometrics		
1. Standard length	303.6	117.0	122.1	65.9–303.6
2. Greatest body depth	39.2	47.3	44.7	41.5–49.6
3. Predorsal length	46.4	48.3	47.9	47.0–50.8
4. Dorsal-fin base length	18.0	19.7	20.1	17.9–20.8
5. Dorsal fin to adipose fin distance	25.0	23.3	23.8	21.6–26.0
6. Dorsal fin to caudal fin distance	42.0	41.1	41.1	39.5–43.2
7. Prepelvic length	49.3	52.0	51.0	49.2–56.8
8. Preanal length	76.4	79.0	77.1	76.9–81.2
9. Snout to anal-fin insertion	79.3	82.6	79.7	78.5–83.9
10. Anal-fin base length	9.7	10.8	11.9	10.2–12.1
11. Caudal-peduncle length	15.2	14.3	14.9	12.5–15.2
12. Dorsal-fin length	25.7?	46.7	34.6	31.8–46.2
13. Pectoral-fin length	15.5?	20.9	21.0	18.4–24.2
14. Pelvic-fin length	15.5?	26.2	18.9?	19.3–33.3
15. Least caudal-peduncle height	9.5	12.5	11.8	10.9–12.7
16. Head length	29.5	30.5	30.7	29.1–34.4
17. Snout length	39.5	35.6	35.7	32.2–40.3
18. Bony orbital diameter	21.5	25.5	26.9	21.5–37.6
19. Postorbital length	44.2	38.7	41.9	34.0–41.7
20. Interorbital width	53.9	53.5	50.9	47.3–57.0
21. Mouth width	40.3	46.8	43.5	41.3–50.3
		Meristics		
Lateral-line scales	59	61	63	56–68
Scale rows between dorsal-fin origin and lateral line	13	13	12	11–13
Scale rows between anal-fin origin and lateral line	11	10	11	10–12
Scale rows between pelvic-fin insertion and lateral line	13	13	13	12–14
Rows of scales around caudal peduncle	25	24	24	23–27
Median predorsal scales	18	16	17	13–18
Median scales between dorsal and adipose fins	17	15	16	15–19
Vertebrae	–	37	37	36–37
Inner row teeth, upper jaw	–	9	9	8–11
Inner row teeth, lower jaw	–	7	7	5–9

compressed; greatest body depth at dorsal-fin origin. Dorsal profile of head concave. Predorsal profile of body convex, distinctly posteroventrally inclined at dorsal-fin base; body profile straight between posterior of dorsal-fin base and adipose-fin origin, and concave along caudal peduncle. Predorsal portion of body with middorsal ridge. Postdorsal portion of body transversely rounded. Ventral profile of body strongly convex from posterior portion of lower jaw to anal-fin base. Ventral profile of caudal peduncle concave. Prepelvic region transversely flattened proximate to pelvic-fin insertion. Well-developed median keel present between pelvic-fin insertion and anus.

Head pointed in lateral profile. Mouth terminal. Snout length slightly greater than, or equal to, horizontal width of orbit; nares on each side of head close to each other; anterior nares circular, posterior nares crescent shaped. Adipose eyelid present, but poorly developed; most developed anteriorly but with much of eye uncovered. Lips fleshy, less developed than in *Ichthyoelephas* and *Prochilodus,* but forming oral disk when mouth protracted.

Functional teeth in two rows in each jaw. All teeth movably implanted in flesh that overlies jaws. All teeth of similar size, with exposed portions spoon shaped except when worn down. Inner tooth series of each jaw with 8 to 11 teeth on left side of upper jaw and 5 to 9 teeth on left side of lower jaw. Outer row of teeth in each jaw with approximately 76 teeth on each side of upper jaw and approximately 65 teeth on each side of lower jaw in lectotype of *S. squamilentus.* Upper and lower lips bordered by numerous globular, fleshy papillae.

Scales cycloid. Lateral line with 56 to 68 (29.6% of specimens with 58) pored scales; 11 to 13 (62.9% of specimens with 12) horizontal rows of scales between dorsal-fin origin and lateral line; 12 to 14 (66.7% of specimens with 13) horizontal

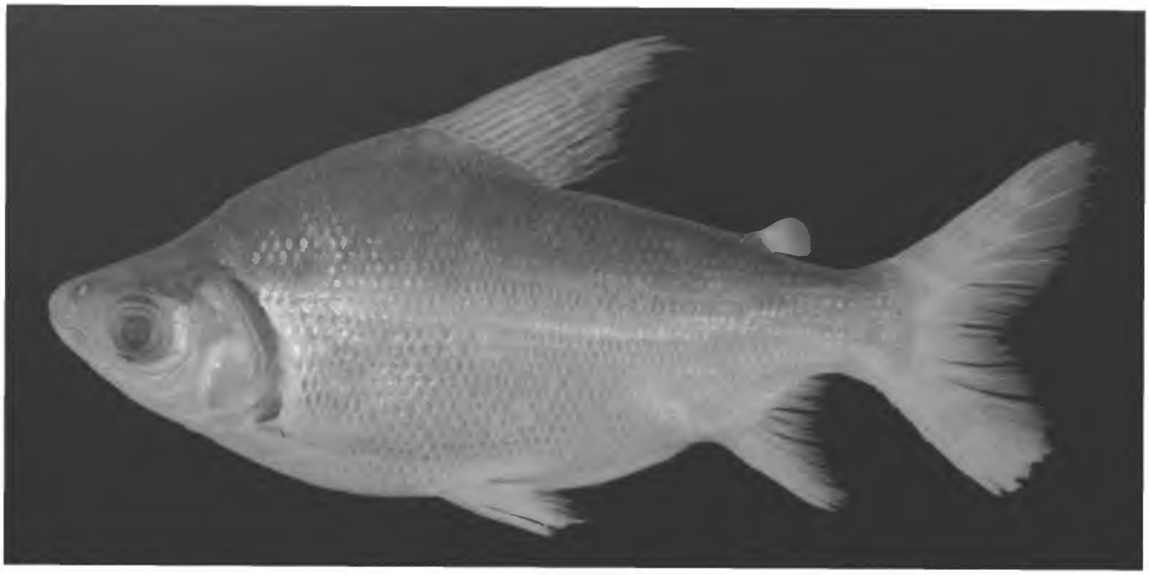


FIGURE 60.—*Semaprochilodus brama*, MZUSP 36852, 193.2 mm SL; Brazil, Pará, Cachoeira do Espelho, Rio Xingú.

rows of scales between pelvic-fin insertion and lateral line; 10 to 12 (70.4% of specimens with 11) horizontal rows of scales between anal-fin origin and lateral line; 13 to 18 (33.3% of specimens with 15) median predorsal scales; 15 to 19 (40.0% of specimens with 17) horizontal rows of scales in middorsal series between posterior of dorsal-fin base and adipose-fin origin; 23 to 27 (48.1% of specimens with 24) horizontal rows of scales around caudal peduncle.

Dorsal fin preceded by small, but well-developed, anteroventrally bifurcate, procumbent spine somewhat triangular in lateral view. Dorsal-fin rays (including procumbent spine) iii,10 [iii,10]; anal-fin rays iii,8 [iii,8]; pectoral-fin rays i,13 to 17 (i,15 most frequent) [i,14]; pelvic-fin rays i,8 [i,8]; principal caudal-fin rays 10/9 [10/9].

Vertebrae 36 or 37 (84.0% of specimens with 37).

Dorsal fin distally pointed; posterior unbranched and anterior branched rays longest and subequal. Dorsal-fin origin closer to tip of snout than to caudal-fin base. Greatest length of adipose fin approximately two-thirds of horizontal width of orbit. Adipose-fin origin located approximately at vertical that passes though middle of anal-fin base. Pectoral fin distally pointed. Tip of adpressed pectoral fin reaching, or almost reaching, pelvic-fin insertion. Pelvic fin falcate. Pelvic-fin insertion located slightly posterior of vertical that passes through dorsal-fin origin. Tip of adpressed pelvic fin reaching posteriorly to region from one-half distance from fin insertion to anus to as far as middle of anal-fin base. Axillary scale present, its length approximately one-fourth or less of greatest length of pelvic fin. Posterior unbranched and anterior branched anal-fin rays longest and subequal. Caudal fin moderately bifurcate.

COLORATION IN ALCOHOL.—Ground coloration golden brown or silvery brown, with dorsal portions of head and body darker. Lateral surface of body with approximately 8 to 16 dark, wavy, horizontal stripes along dorsal and ventral margins of exposed portions of scales. Four to 7 wavy stripes dorsal to, and 4 to 9 wavy stripes ventral to, lateral line. Dense field of brown or black chromatophores forming dark, well-defined area on membranous posterior portion of opercle and on exposed lateral surface of pectoral girdle.

Dorsal fin with 3 to 5 (most frequently 3) dark, irregular stripes beginning on anterior margin of fin and extending across fin approximately parallel to base of fin. Adipose fin with dorsal margin finely outlined with black. Pectoral and pelvic fins hyaline. Base coloration of anal fin hyaline with fields of dark chromatophores forming 1 to 4 (most frequently 3) irregular oblique stripes across fin, with anterior stripes that run in parallel. Caudal fin with 7 to 10 (most frequently 8) dark stripes; 1 horizontal stripe extending over middle caudal-fin rays, with 3 to 5 (most frequently 4) oblique stripes on upper lobe of caudal fin and 3 to 5 (most frequently 3) oblique stripes on lower lobe of fin. Larger and older specimens with pattern of dark stripes across caudal and anal fins becoming fainter, sometimes to point of being almost imperceptible. Iris reddish brown, with diffuse darker areas on dorsal and ventral portions.

COLORATION IN LIFE.—(Based upon photographs of recently captured specimens from the Rio Xingu basin provided by Jansen A.S. Zuanon, INPA). Overall pigmentation bright silvery,

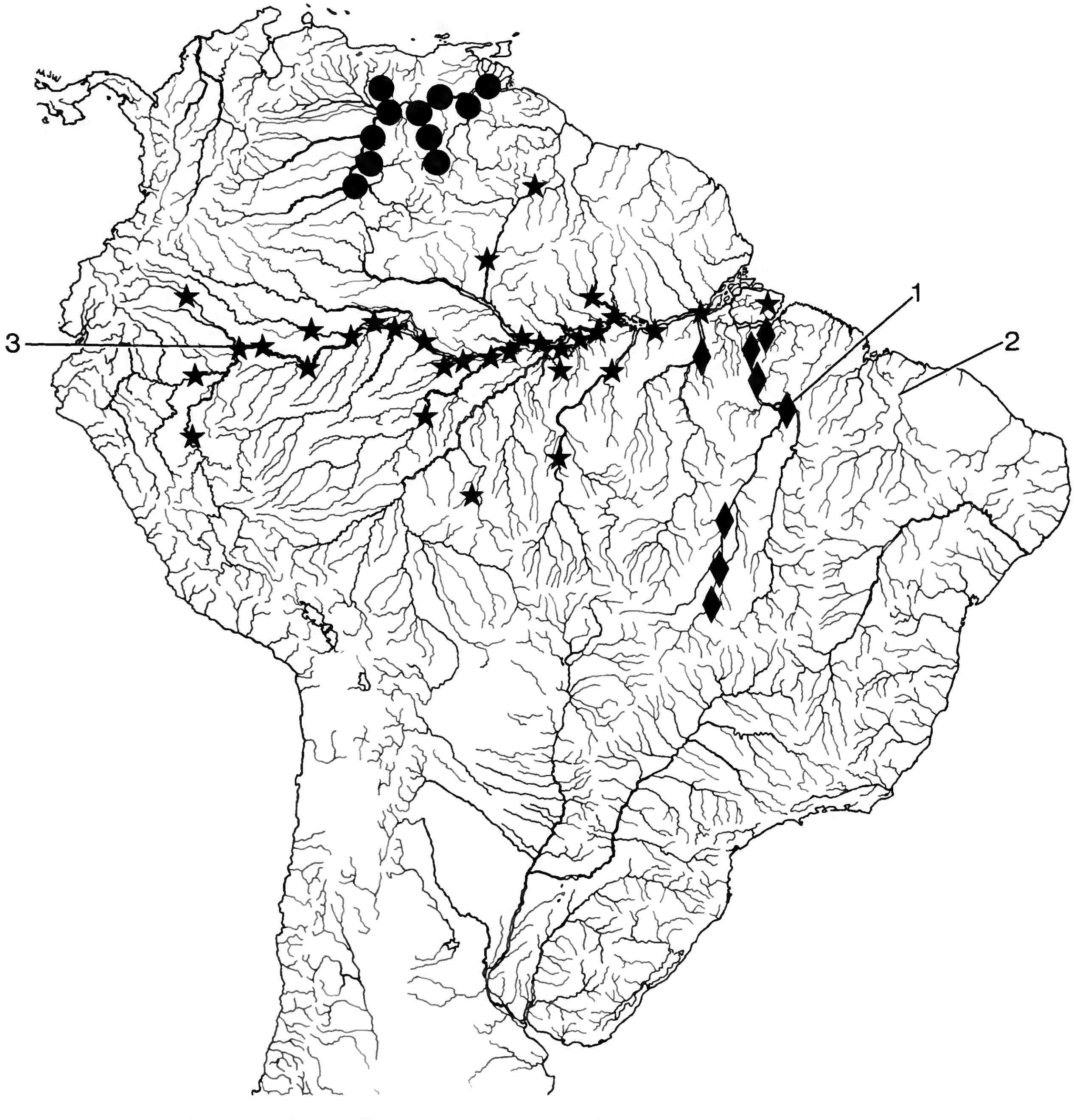


FIGURE 61.—Map of central and northern South America showing geographic distribution of *Semaprochilodus brama* (diamonds; 1=holotype locality, 2=reported holotype locality of *Semaprochilodus squamilentus*, see text for discussion of problems with reported locality), *Semaprochilodus insignis* (stars; type locality of *Semaprochilodus insignis* inexact=Rio Branco (=Brazil, Roraima, Rio Branco); 3=holotype locality of *Prochilodus theraponura;* holotype locality of *Prochilodus amazonensis* inexact=lower Amazons), and *Semaprochilodus kneri* (dots; type locality inexact=Orénoque (=Río Orinoco)) (some symbols represent more than one collecting locality and/or lot of specimens).

darker dorsally on body and particularly on postorbital portion of head. Dark band along margin of opercle particularly apparent. Pelvic fins reddish. Anal fin reddish on distal portions of middle fin rays (full extent of red pigmentation cannot be determined because of damage to fin). Caudal fin with reddish band extending across most of posterior one-half of fin, but with red pigmentation separated from distal margin of fin by hyaline bar. Hyaline region about two-thirds of eye diameter and with distinct posterior margin in upper lobe of caudal fin. Red pigmentation less obvious on lower lobe of caudal fin and with less distinct border relative to distal hyaline bar.

DISTRIBUTION.—*Semaprochilodus brama* is apparently limited to the clear-water Rio Xingu and Rio Tocantins basins, Brazil (Figure 61, diamonds).

COMMON NAME.—Jaraqui (Brazil).

COMPARISONS.—A noted in the "Diagnosis," above, *Semaprochilodus brama* is unequivocally distinguishable from all congeners on the basis of details of various pigmentation and diverse meristic features.

BIOLOGY AND FISHERIES.—According to Mendes dos Santos et al. (1984:27), *Semaprochilodus brama* demonstrates a complex migration pattern associated with reproduction and feeding. The species is very important in the commercial fishery in the Rio Tocantins basin, accounting for 15% of the total commercial landings.

REMARKS.—The description of *Prochilodus brama* Valenciennes (1850:82–84) was based upon one specimen collected by Deville and Castelnau in the "l'Amazone" (=Rio Amazonas, more specifically in the Rio Tocantins, at São João das Duas Barras (= São João do Araguaia), in the state of Pará, Brazil). The holotype, MNHN A.1066, 303.6 mm SL, is an eviscerated and mostly defleshed, dried specimen stuffed with straw, but it is otherwise in reasonable condition in light of its age. Neither the caudal nor the anal fins of the holotype demonstrate the obvious dark stripes present in smaller individuals of the species, and Valenciennes (1850:84) explicitly stated, "I do not see any marks on the fins" (our translation). Nonetheless, we confidently identity the holotype as assignable to *Semaprochilodus* because of its possession of cycloid scales with a spatulate membranous process on the posterior border of each scale along the middorsal series between the posterior of the dorsal-fin base and the adipose-fin origin, the relative size of the lips, and the various scale counts. The holotype of *S. brama* is the largest specimen of the species examined in this study, and conspecifics of body sizes approaching that of the holotype frequently have only very faint or in some cases effectively absent dark bands across the anal and caudal fins (see Figure 60). A tendency towards the ontogenetic loss in the degree of distinctiveness of the anal and caudal fin pigmentation patterns characteristic for the species of *Semaprochilodus* would have been exacerbated in the case of the holotype of *S. brama* by its dessication during preservation. This tendency for an ontogenetic loss of the caudal and anal fin pigmentation in large specimens of *S. brama* may account for the continued assignment of *S. brama* to *Prochilodus,* the members of which lack dark stripes on the anal and caudal fins, even after Mago-Leccia (1972:44, 58) utilized the presence of such fin pigmentation as one of the features that delimits *Semaprochilodus*. The first authors to formally propose that the species should be shifted from *Prochilodus* to *Semaprochilodus* were Santos et al. (1984:27).

Fowler's (1941:171–174, fig. 83) description of *Semaprochilodus squamilentus* was based upon two specimens sent by von Ihering that purportedly originated in the Rio Parnaíba, at Terezina, Piauí, Brazil. *Semaprochilodus squamilentus* is actually a junior synonym of *S. brama,* as demonstrated by the data presented in Table 18 and by the details of its pigmentation and body form. The stated type locality for *S. squamilentus* is problematic in light of the fact that all specimens of *S. brama* with exact locality information originated either in the Rio Xingu of the Amazon basin or the Rio Tocantins system, both of which lie to the west of, and are noncontiguous with, the Rio Parnaíba drainage that empties independently into the Atlantic Ocean.

Other specimens that supposedly originated in northeastern Brazil and that were sent by von Ihering to Fowler were probably collected in the Rio Tocantins or Rio Amazonas basins (see comments in Vari (1995:80) and in Vari and Harold (2001:46) and references therein). Except for the citation by Fowler (1941:172) and those of subsequent authors based upon Fowler, we were unable to locate any references in the literature for the occurrence of *Semaprochilodus* in the Rio Parnaíba system. Furthermore, no specimens of *Semaprochilodus* that originated in the Rio Parnaíba basin were encountered during this study. Equally noteworthy is the absence of references to *Semaprochilodus* in the fisheries literature for the Rio Parnaíba basin. Such a lapse would be extremely unlikely if *Semaprochilodus* were present in that drainage system in light of the relatively large body sizes attained by members of the genus, including *S. brama,* and their importance in both subsistence and commercial fisheries. The overall evidence indicates that *Semaprochilodus* does not occur in the Rio Parnaíba of northeastern Brazil. The type material of *S. squamilentus,* presumably actually originated in the Rio Tocantins or Rio Xingu basins, and the species is herein considered to be a synonym of *S. brama,* which is endemic to those river basins.

The description of *Prochilodus dobulinus* Valenciennes (1850:81–82) was based upon a specimen collected by Castelnau in the Rio Araguaia, Brazil. The holotype of the species was not reported by Bertin (1947) in his listing of the characiform types in the Museum National d'Histoire Naturelle (MNHN), nor have subsequent attempts to locate the specimens proved successful. In commenting on the holotype, Valenciennes (1850:82), however, noted that "the scales are a bit smaller and smoother. We count fifty along the lateral line. The color appears to have been a uniform silver. There is no spot on the fins" (our translation). Only two prochilodontid species, *Prochilodus lineatus* and *Semaprochilodus brama,* are known from the Rio Tocantins basin, the system that includes the Rio Araguaia. The information provided by Valenciennes is equivocal as to which of these might be the senior synonym of *Prochilodus dobulinus*. Although the reported number of lateral-line scales in the holotype of that species (50) falls within the range for that feature in *P. nigricans* (44–51) and outside the range for *Semaprochilodus brama,* Valenciennes reported that in *Prochilodus dobulinus* the scales are smoother than in other *Prochilodus,* a characterization more in keeping with the condition in the species of *Semaprochilodus*. Given these inconsistencies, we consider *Prochilodus dobulinus* to be a nomen dubium, and a resolution of the question of the identity of this nominal form can only be arrived at via the rediscovery of the holotype of the species.

MATERIAL EXAMINED.—64 specimens (26, 65.9–303.6 mm SL).

BRAZIL. *Goiás:* Rio Araguaia, near Aruanã (14°58′S, 51°24′W), USNM 191636, 1 (65.9) [1R]. Lago Rico, near Cocalinho, Rio Araguaia, MZUSP 21537, 3 (2, 241.7–287.5) [2R]. *Mato Grosso:* Santa Terezinha, Rio Araguaia, MZUSP 20835, 1 (1, 99.4) [1R]. *Pará:* Baião, Rio Tocantins, UMMZ 203535, 2 (2, 98.7–112.4) [2R]. Igarapé do Limão, Rio Tocantins, Baião, MZUSP 21260, 4 (4, 85.3–115.3) [4R]. Marginal lagoon of Rio Tocantins, near Baião, MZUSP 21266, 4 (1, 90.5–113.6). Lago Trocará, below Tucuruí (approximately 3°42′S, 49°47′W), MZUSP 21340, 1 (1, 191.0). Small lagoon near Tucuruí, Rio Tocantins (3°42′S, 49°47′W), MZUSP 21331, 5 (5, 108.9–120.1) [5R]. Igarapé Aricurá, Cametá, MZUSP 21257, 5 (82.4–120.7). Igarapé Maloca, Rio Tocantins, near Cametá (2°15′S, 49°30′W), MZUSP 21254, 8 (2, 72.7–96.2), MZUSP 42716, 2 (cleared and counterstained for bone and cartilage). Marginal lagoon of Igarapé Muru, Rio Tocantins, below Tucuruí (approximately 3°42′S, 49°47′W), MZUSP 21286, 1 (1, 105.9). São João do Araguaia (previously named São João das Duas Barras), Rio Tocantins, MNHN A.1066, 1 (1, 303.6, holotype of *Prochilodus brama*). Abaetetuba (market), MZUSP 21240, 7 (134.6–147.0). Paraná Samuuma, mouth of Rio Tocantins, MZUSP 21251, 7 (126.3–145.4). Igarapé Oxipucu, Mocajuba, Rio Tocantins, MZUSP 21259, 2 (2, 112.0–124.8) [2R]. Igarapé Pindobazinho, mouth of Rio Tocantins, MZUSP 21248, 2 (2, 126.8–130.3) [2R]. Cachoeira do Espelho, Rio Xingú, MZUSP 36852, 4 (2, 181.8–207.6) [2R]. Igarapé Sororoca, furo de Panaquera, MZUSP 21243, 1 (164.3). *Erroneous Locality:* "Rio Parnahyba, Therezina, Piauhy, eastern Brazil" (= Rio Parnaíba, Terezina, Piauí, Brazil; corrected herein to Brazil, Rios Tocantins and Araguaia), ANSP 69480, 1 (1, 117.0, holotype of *Semaprochilodus squamilentus;* see under "Remarks," above, concerning apparently erroneous purported type locality) [1R]; ANSP 69481, 1 (1, 122.1, paratype of *Semaprochilodus squamilentus;* see under "Remarks," above, concerning apparently erroneous purported type locality) [1R]. *Inexact Locality:* Barcarena fish market (specimen said to have originated in the Rio Tocantins), USNM 295160, 1.

***Semaprochilodus insignis* (Jardine, 1841)**

FIGURES 61, 62; TABLE 19

Prochilodus insignis Jardine, 1841:261, pl. 30 [type locality: Rio Branco (= Brazil, Roraima, Rio Branco)].—Valenciennes in Cuvier and Valenciennes, 1850:88 [Rio Branco].—Kner, 1859:147 [Rio Negro].—Günther, 1864:296 [(Brazil), Santarem].—Cope, 1872:258 [Peru, Ambiyacu River].—Steindachner, 1881:128 [in part; cited specimens from (Brazil) Óbidos and Teffé (= Tefé), reported distribution other than for cited occurrence of species in Guiana].—Eigenmann and Eigenmann, 1891:48 [in listing of South American fishes].—Regan, 1905:189 [Rio Negro; based upon Wallace drawings].—Fowler, 1906:315 [*Prochilodus theraponura* provisionally separated from *P. insignis*]; 1940a:260 [compared with *P. theraponura* and *P. amazonenis*]; 1950:219 [literature compilation]; 1975:359 [literature compilation].—Eigenmann, 1907b:768 [lateral-line scale count]; 1910:424 [in listing of South American fishes; in part, not listing of species as occurring in Guianas]; 1912:20 [Rio Branco].—Eigenmann and Ogle, 1907:5 [Bolivia].—Pellegrin, 1909b:153 [in part, not specimen from French Guiana].—Magalhães, 1931:241 [common name].—Eigenmann and Allen, 1942:46 [Peru, lower Río Marañon basin].—Lowe-McConnell, 1964:119 [Guyana, Rupununi Savanna].—Kastberger, 1978:54 [sound production].

Salmo jaraqui Kner, 1859:148 [name in discussion of *Prochilodus binotatus*].

Prochilodus theraponura Fowler, 1906:313, fig. 14 [type locality: Ambiyacu River Equador (= Peru, Loreto, Río Ampiyacu, near Pebas (Pevas)); species provisionally separated from *P. insignis*]; 1940a:260 [Peru, Río Ucayali basin, Contamana]; 1945:122 [Peru]; 1950:225 [literature compilation]; 1975: 360 [literature compilation].—Eigenmann, 1907b:768 [cited as probable synonym of *Prochilodus insignis* Jardine, 1841].—Pellegrin, 1909b:154 [as valid species].—Géry, 1977:218 [middle and upper Amazon].—Böhlke, 1984:148 [holotype despository].

Prochilodus amazonensis Fowler, 1906:316, fig. 15 [type locality: lower Amazons (= lower Rio Amazonas); cited as closely related to *Prochilodus insignis*]; 1911:497 [comparison with *Prochilodus stigmaturus*]; 1940a:260 [Peru, Río Ucayali basin, Boca Chica]; 1945:122 [Peru].—Eigenmann, 1907b:768 [cited as probable synonym of *Prochilodus insignis* Jardine, 1841].—Pellegrin, 1909a:148 [Brazil: Santarém, Teffé (= Tefé), Tabatinga, Tonnantins]; 1909b:154 [Brazil: Santarém, Teffé (= Tefé), Tabatinga, Tonnantins].—Eigenmann and Allen, 1942:46 [Peru, lower Río Marañon basin].—Géry, 1972a:149, fig. 12 [predorsal procumbent spine].—Mago-Leccia, 1972:59 [as possible synonym of *Prochilodus theraponura*].

Prochilodus teraponura.—Fowler, 1911:497 [comparison with *Prochilodus stigmaturus;* species name incorrectly spelled].

Prochilodus binotacus [not of Jardine, 1841].—Magalhães, 1931:128 [unjustified emendation; common name].

Prochilodus theraponeura.—Eigenmann and Allen, 1942:46 [unjustified emendation of species name; Peru, lower Río Marañon basin].

Prochilodus amazonicus.—Eigenmann and Allen, 1942:48 [unjustified emendation of species name; Peru, lower Río Ucayali basin].

Semaprochilodus amazonensis.—Fowler, 1950:227 [literature compilation]; 1975:361 [literature compilation].—Mago-Leccia, 1972:58 [as synonym of *S. theraponura*].—Ortega and Vari, 1986:11 [Peru; common name].—Castro, 1988:504 [comparison with *Semaprochilodus varii*].

Semaprochilodus insignis.—Mago-Leccia, 1972:58 [as recognized species of *Semaprochilodus*].—Roberts, 1973b:214 [nocturnal spawning].—Goulding, 1980:244 [feeding habits].—Smith, 1981:12 [spawning season].—Lowe-McConnell, 1984:143 [economic importance].—Nomura, 1984:58 [Brazil, common name].—Araújo-Lima, 1985:423 [larval development].—Ribeiro, 1985: 419 [interbreeding with *Semaprochilodus taeniurus*].—Feldberg et al., 1986:1 [cytogenetics].—Araújo-Lima and Hardy, 1987:127 [ontogenetic changes in food habits].—Stewart et al., 1987:23 [Ecuador, Río Napo].—Bayley, 1988:131, table 2 [growth rates].—Castro, 1988:503 [literature citations of the species for Guiana indicated as misidentifications].—Petrere, 1989:5 [economic importance at Manaus, Brazil, fish market].—Vazzoler et al., 1989:165 [Brazil, Rio Negro basin; reproductive biology].—Vazzoler et al., 1989:175 [Brazil, Rio Negro; spawning periods].—Ribeiro and Petrere, 1990:195 [fisheries ecology and management].—Vazzoler and Amadio, 1990:537 [schooling behavior and structure].—Menezes and Vazzoler, 1992: 64 [reproductive characteristics].—Araújo-Lima, 1994:44 [egg size and development].—Ferreira et al., 1998:41, fig. 16 [Brazil, Amazonas, region of Santarém; economic importance in fishery].—Saint-Paul et al., 2000:239, 242 [Brazil, Amazonas, Rio Negro, Lago do Prato; abundance, occurrence in black waters].—Sánchez-Botero and Araújo-Lima, 2001:441 [Brazil, Manaus region; occurrence in aquatic macrophytes].—Wallace, 2002:258, fig. 98 [Javita (= Yavita), sources of Orinoko (= Orinoco)].

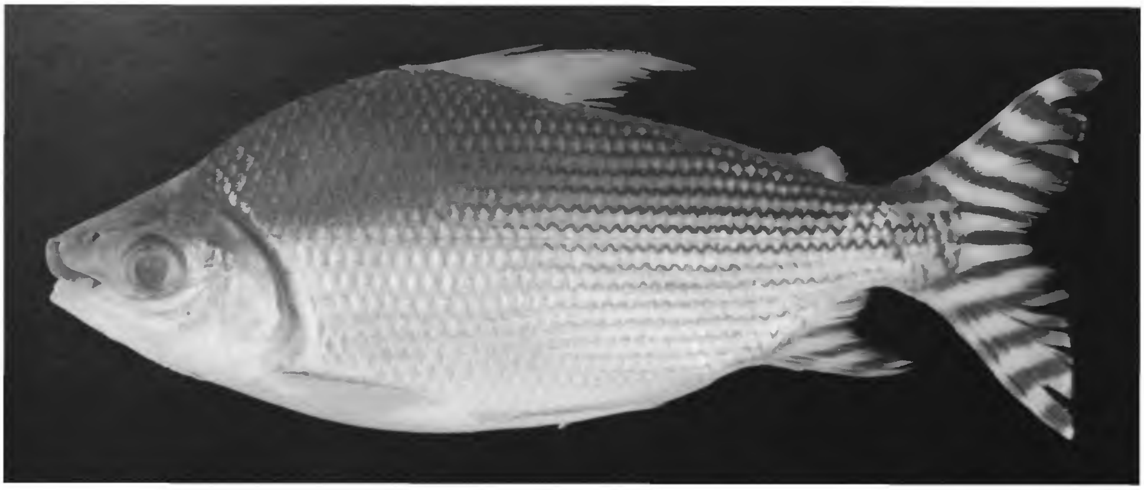


FIGURE 62.—*Semaprochilodus insignis,* USNM 290151, 204.0 mm SL; Brazil, Amazonas, Manaus.

Semaprochilodus theraponura.—Mago-Leccia, 1972:58, as synonym of *Semaprochilodus amazonensis* (Fowler, 1906).—Goulding, 1981:39 [migration in Brazil, Rio Madeira].—Junk et al., 1983:406, table 3 [Brazil, Amazon; ecology].—Ferreira, 1984:355 [Brazil, Santarém].—Géry and Mahnert, 1984:172 [as possible senior synonym of *Semaprochilodus kneri*].—Lowe-McConnell, 1984:143 [economic importance].—Ortega and Vari, 1986:11 [Peru, Amazon basin; common name].

Semaprochilodus sp.—Géry and Mahnert, 1984:173, fig. 1 [Peru, Río Mazan].

Semaprochilodus brama [not of Valenciennes, 1850].—Nomura, 1984:58 [Brazil, common name].

Semaprochilodus insignis x *Semaprochilodus taeniurus.*—Ribeiro, 1985:419 [report on interspecific hybrid in central Amazon].

Semaprochilodus teraponura.—Castro, 1988:504 [compared with *Semaprochilodus varii,* species name misspelled].

DIAGNOSIS.—*Semaprochilodus insignis* can be distinguished from *S. brama, S. laticeps,* and *S. varii* in its lack of the intensely darkly pigmented membranous opercle and exposed surface of the pectoral girdle found in those species and in having 39 to 41 vertebrae contrary to the range of 35 to 37 vertebrate found in those three species in combination. *Semaprochilodus insignis* differs, in turn, from *S. taeniurus* in the number of scales along the lateral line (47 to 53 versus 64 to 77, respectively), the number of horizontal rows of scales between the dorsal-fin origin and the lateral line (9 to 11 versus 12 to 14), and the number of horizontal rows of scales between the pelvic-fin insertion and the lateral line (9 to 11 versus 12 to 14, respectively). Finally, *Semaprochilodus insignis* of the Rio Amazonas system differs from *S. kneri,* which is endemic to the Río Orinoco basin, in the number of horizontal rows of scales between the anal-fin origin and the lateral line (7 to 9, 8 most frequent, versus 6 or 7, 6 most frequent, and 7 in only 21% of the 38 specimens examined for this feature, respectively; Figure 63), the number of horizontal scale rows from the dorsal-fin origin to the lateral line (9 to 11, 10 most frequent and 9 in 16% of the 150 specimens examined for this feature, versus 8 or 9, 8 most frequent and 9 in only 21.0% of the 38 specimens examined for this feature, respectively; Figure 64), the number of horizontal rows of scales between the pelvic-fin insertion and the lateral line (9 to 11, 10 most frequent and 9 in 23.5% of specimens examined for this feature, versus 7 to 9, with 8 most frequent and 9 in only 5.3% of specimens examined for this feature, respectively; Figure 65), the range and mode of the number of lateral-line scales (47 to 53, 48 most frequent and 49 frequent, versus 45 to 49, 47 most frequent and 48 and 49 in only 18.9% of specimens examined for this feature, respectively;

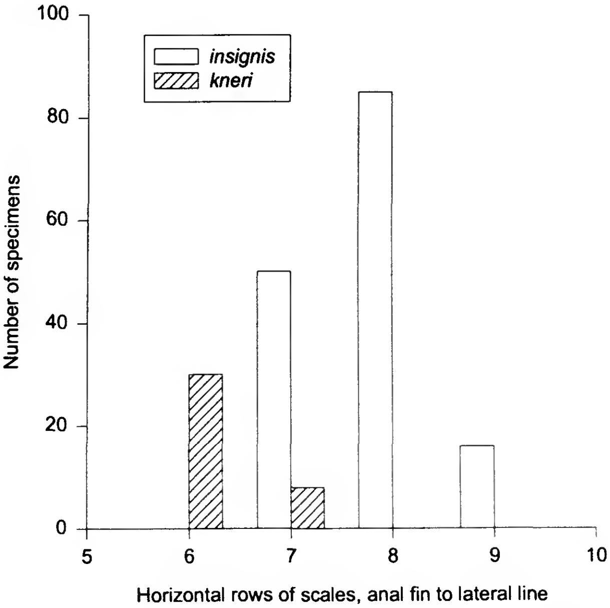


FIGURE 63.—Histogram of number of horizontal rows of scales between anal-fin origin and lateral line plotted against number of specimens with particular counts in *Semaprochilodus insignis* and *Semaprochilodus kneri.*

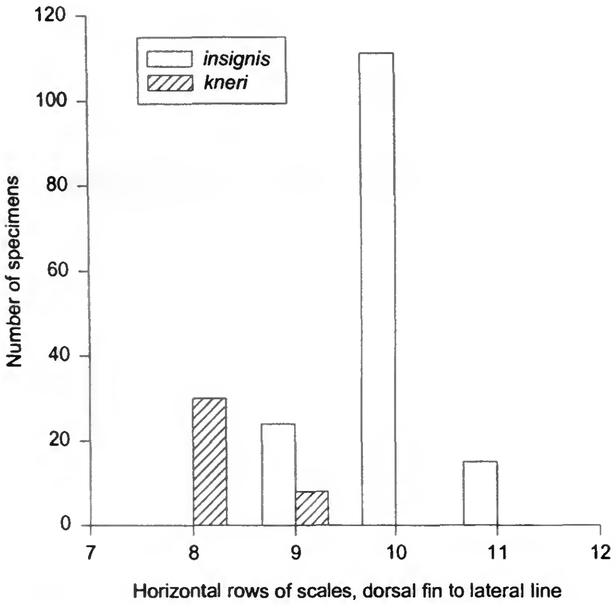


FIGURE 64.—Histogram of number of horizontal rows of scales between dorsal-fin origin and lateral line plotted against number of specimens with particular counts in *Semaprochilodus insignis* and *Semaprochilodus kneri*.

Figure 66), and the form of the vertically expanded articular surface of the uncinate process of the second epibranchial (continuous versus subdivided, respectively).

DESCRIPTION.—Morphometric and meristic data for *Semaprochilodus insignis* presented in Table 19. Body moderately high and compressed laterally. Greatest body depth at dorsal-fin origin. Dorsal profile of head slightly concave. Predorsal profile of body moderately convex. Body profile posteroventrally inclined along dorsal-fin base and ranging from slightly convex to straight from rear of dorsal-fin base to adipose fin and concave along caudal peduncle. Predorsal portion of body with slight predorsal median ridge.Postdorsal portion of body transversely rounded. Ventral profile of body moderately convex from tip of lower jaw to posterior of anal-fin base. Ventral profile of caudal peduncle concave. Prepelvic region transversely flattened proximate to pelvic-fin insertion. Distinct median keel present between pelvic-fin insertion and anus.

Head profile pointed. Mouth terminal. Snout length greater than horizontal width of eye. Nares of each side of head close together; anterior nares circular, posterior nares crescent shaped. Adipose eyelid present, but poorly developed; development greatest anteriorly, but with major portion of eye uncovered. Lips fleshy, less developed than in *Ichthyoelephas* and *Prochilodus* species, but forming oral disk when mouth protracted.

Functional teeth in two rows in each jaw. All teeth movably implanted in flesh that overlies jaws. All teeth of similar size, with exposed portion spoon shaped except when worn down. Inner tooth series in each jaw with 10 to 16 teeth on left side of upper jaw and 6 to 11 teeth on left side of lower jaw. Outer row of teeth in each jaw with approximately 60 to 90 teeth on each side of upper jaw and approximately 56 to 73 teeth on each side of lower jaw in examined type specimens. Upper and lower lips bordered by numerous globular, fleshy papillae.

Scales cycloid. Scales in middorsal series between posterior of dorsal-fin base and adipose-fin origin similar in form to those of adjoining portions of body, but with spatulate, well-developed membranous process along posterior border of each scale in that series. Lateral line with 47 to 53 (36.1% of specimens with 48) pored scales; 9 to 11 (75.7% of specimens with 10) horizontal rows of scales between dorsal-fin origin and lateral line; 9 to 11 (60.9% of specimens with 10) horizontal rows of scales between pelvic-fin insertion and lateral line; 7 to 9 (53.6% of specimens with 8) horizontal rows of scales between anal-fin origin and lateral line; 11 to 15 (45.8% of specimens with 13) median predorsal scales; 13 to 19 (42.4% of specimens with 15) scales in middorsal series between posterior of dorsal-fin base and adipose-fin origin; 18 to 22 (83.8% of specimens with 20) horizontal rows of scales around caudal peduncle.

Vertebrae 39 to 41 (47.8% of specimens with 40 and 41 vertebrae) (38 vertebrae reported by Jardine (1841) in original description; see "Remarks").

Dorsal fin preceded by small, but well-developed, anteroventrally bifurcate, procumbent spine somewhat triangular in lateral view. Dorsal-fin rays (including procumbent spine) iii,9 or 10 (iii,10 most frequent) (9 rays reported by Jardine (1841) in

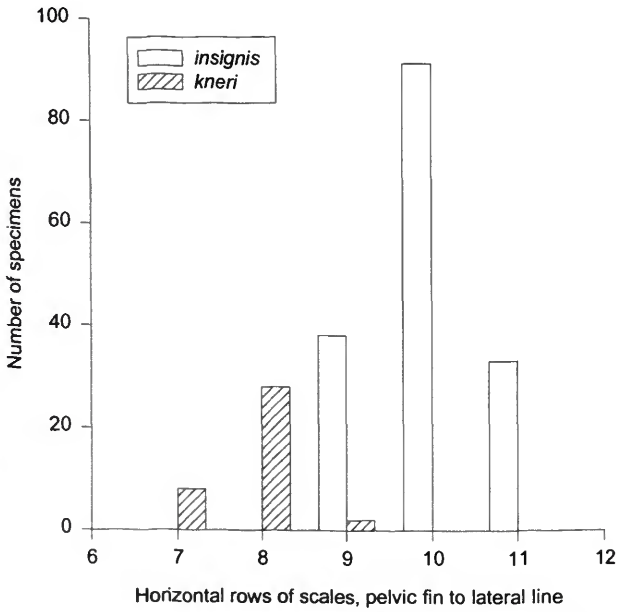


FIGURE 65.—Histogram of number of horizontal rows of scales between pelvic-fin insertion and lateral line plotted against number of specimens with particular counts in *Semaprochilodus insignis* and *Semaprochilodus kneri*.

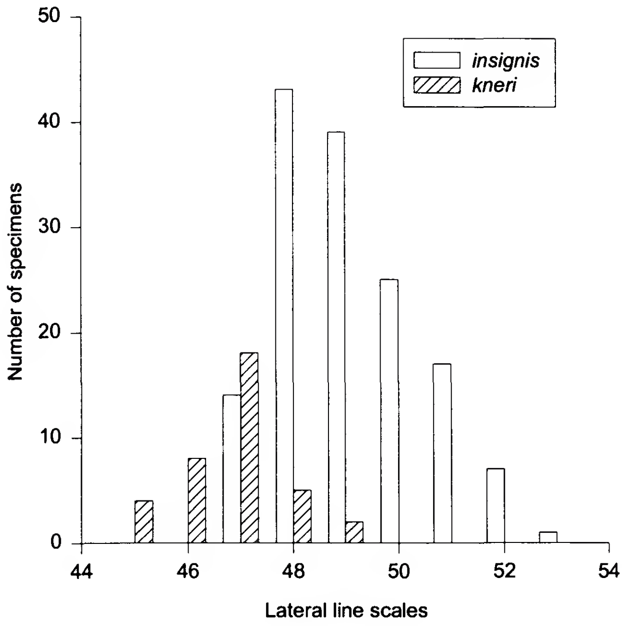


FIGURE 66.—Histogram of number of lateral-line scales plotted against number of specimens with particular counts in *Semaprochilodus insignis* and *Semaprochilodus kneri.*

TABLE 19.—Morphometrics and meristics of *Semaprochilodus insignis:* (A) holotype of *Prochilodus amazonensis,* ANSP 21350; (B) holotype of *Prochilodus theraponura,* ANSP 8033; and (C) all specimens of *Semaprochilodus insignis* from which counts and measurements were taken. Standard length is presented in mm; values 2 to 16 are percentages of SL, 17 to 21 are percentages of HL. Question mark indicates specimen damaged for the indicated feature.

Characters	A	B	C
	Morphometrics		
1. Standard length	89.5	42.6	22.0–305.3
2. Greatest body depth	42.8	42.0	33.5–50.7
3. Predorsal length	46.8	47.9	35.1–53.1
4. Dorsal-fin base length	17.9	18.8	16.0–19.8
5. Dorsal fin to adipose fin distance	25.4	25.1	19.1–30.9
6. Dorsal fin to caudal fin distance	43.9	38.5	34.5–47.9
7. Prepelvic length	53.9	55.2	49.0–62.5
8. Preanal distance	76.4	77.2	72.0–81.3
9. Snout to anal-fin insertion	80.2	80.0	77.3–85.9
10. Anal-fin base length	10.8	9.9	7.9–12.3
11. Caudal-peduncle length	14.9	12.4	7.9–16.7
12. Dorsal-fin length	28.7?	25.4	25.4–71.6
13. Pectoral-fin length	21.2	12.2?	14.0–23.0
14. Pelvic-fin length	15.8?	15.5?	15.3–25.4
15. Least caudal-peduncle height	10.7	10.8	9.4–13.2
16. Head length	30.7	34.7	24.7–39.6
17. Snout length	34.2	31.8	26.3–42.9
18. Bony orbital diameter	30.5	31.8	21.3–39.0
19. Postorbital length	40.0	41.2	29.3–46.1
20. Interorbital width	49.1	45.3	33.6–54.5
21. Mouth width	42.5	35.1	29.1–48.9
	Meristics		
Lateral-line scales	48	46?	47–53
Scale rows between dorsal-fin origin and lateral line	11	10?	9–11
Scale rows between anal-fin origin and lateral line	8	8?	7–9
Scale rows between pelvic-fin insertion and lateral line	10	10?	9–11
Rows of scales around caudal peduncle	20	18?	18–22
Median predorsal scales	14	12?	11–15
Median scales between dorsal and adipose fins	15	15?	13–19
Vertebrae	41	40	39–41
Inner row teeth, upper jaw	11	14	10–16
Inner row teeth, lower jaw	10	11	6–11

original description, a count that presumably included branched and unbranched rays); anal-fin rays iii,7 to 9 (iii,8 most frequent) (9 rays reported by Jardine (1841) in original description, a count that presumably included branched and unbranched rays); pectoral-fin rays i,12 to 16 (i,15 most frequent) (14 rays reported by Jardine (1841) in original description, a count that presumably included branched and unbranched rays); pelvic-fin rays i,7 or 8 (i,8 most frequent) (8 rays reported by Jardine (1841) in original description); principal caudal-fin rays 10/9.

Dorsal fin distally pointed; posterior unbranched and anterior branched rays longest and subequal; dorsal-fin origin closer to tip of snout than to caudal-fin base. Greatest length of adipose fin approximately equal to three-fourths of horizontal width of orbit; adipose-fin origin located along vertical that passes though mid-length of anal-fin base. Pectoral fin pointed distally. Tip of adpressed fin extending posteriorly to, or almost to, pelvic-in origin. Pelvic fin falcate. Pelvic-fin insertion located along vertical that passes through anterior one-third of dorsal-fin base. Tip of adpressed pelvic fin extending posteriorly approximately two-thirds of distance between pelvic-fin insertion and anus. Axillary scale present, length of scale approximately one-third of pelvic-fin length. Posterior unbranched and anterior branched anal-fin rays longest and subequal. Caudal fin moderately bifurcate.

COLORATION IN ALCOHOL.—Ground coloration yellowish gold, with dorsal portions of head and body darker. Lateral surface of body with approximately 7 to 12 dark, wavy, horizontal stripes along dorsal and ventral margins of exposed portions of scales. Approximately 4 to 7 wavy stripes dorsal to, and 2 to 7 wavy stripes ventral to, lateral line; stripes somewhat irregular on caudal peduncle. Diffuse fields of brown chromatophores on membranous portion of rear of opercle and on exposed lateral portion of pectoral girdle.

Dorsal fin with 3 to 6 (most frequently 3) dark, irregular stripes beginning on anterior margin of fin and extending across fin approximately parallel to base of fin. Adipose fin with posterodorsal border darkened. Pectoral and pelvic fins hyaline. Ground pigmentation of anal fin mostly hyaline, but with fields of dark chromatophores forming 1 to 5 (most frequently 3) irregular dark stripes; anterior stripes parallel. Anal-fin stripes occasionally absent. Caudal fin with 4 to 14 (most frequently 7) dark stripes; one horizontal stripe overlying median caudal-fin rays; 2 to 7 (most frequently 3) oblique stripes on upper lobe of caudal fin and 2 to 7 (most frequently 4) oblique stripes on inferior lobe. Iris yellowish golden, with darker diffuse areas on dorsal and ventral portions.

COLORATION IN LIFE.—(Based upon color transparency by the first author of a recently collected adult specimen from Lago Janauacá, along the Rio Solimões, in the central portion of the Amazon basin). Dark pigmentation as described above. Ground coloration silvery. Dorsal portion of head and body, particularly head, darker. All fins notably yellow, with intensity of pigmentation somewhat less developed on pectoral and pelvic fins and with those fins, particularly pelvic fins, reddish along borders and on distal portions. Iris golden brown. Coloration of recently collected specimen illustrated by Ferreira et al. (1988, fig. 41).

DISTRIBUTION.—*Semaprochilodus insignis* occurs in the central portions of the Rio Amazonas system and most of its major black- and white-water tributaries, including the Rio Negro, Rio Branco, Rio Madeira, Rio Tapajós, Rio Purus, Rio Içá, and the Río Napo, Río Marañon, and Río Ucayali (Figure 61, stars). Within the Amazon basin, *S. insignis* is strikingly absent in the clear-water Rio Xingú and Rio Tocantins basins (Ziesler and Ardizzone, 1979), which are inhabited by *S. brama*—a species apparently endemic to those river systems.

COMMON NAME.—Jaraqui, jaraqui-da-escama-grossa (Brazil) and yhuarachi (Peru).

COMPARISONS.—*Semaprochilodus insignis* differs unequivocally from all congeners except *S. kneri* in various meristic and/or pigmentary features. Those two nominal species differ in the ranges and modes of various features (see "Diagnosis," above) and have totally allopatric distributions in the Rio Amazonas and Río Orinoco basins, respectively; consequently, they are considered to be distinct species herein.

BIOLOGY AND FISHERIES.—Ribeiro and Petrere (1990) provided a summary of the life history and fishery for *Semaprochilodus insignis* in the central portions of the Amazon basin. In that region, this species and *S. taenurius*, together identified under the common name of jaraquis, "dominate 90 per cent of the commercial fisheries" (Ribeiro and Petrere, 1990:208).

REMARKS.—Many previous authors have cited the authorship of *P. insignis* as either Schomburgk or Jardine and Schomburgk, in Schomburgk. Although the specimens, illustrations, and natural history notes that served as the basis for the 1841 description of *P. insignis* were collected or prepared by Schomburgk, there is no indication in the published text that he actually collaborated with Jardine in the formal original description of that species. We consequently follow Kullander and Stawikowski (1997) and Stawikowski and Kullander (1997) in considering Jardine to be the author of *P. insignis*.

Jardine's (1841:261, pl. 30) description of *Prochilodus insignis* was based upon material collected by Schomburgk in the Rio Branco, Roraima, Brazil. We were unable to locate type specimens of this species in depositories known to hold Schomburgk collections, and no types are cited by Eschmeyer et al. (in Eschmeyer, 1998:778). It thus seems likely that no types are extant for *P. insignis*, a situation that parallels that for other species collected by Schomburgk and described by Jardine. Two *Semaprochilodus* species, *S. insignis* and *S. taeniurus*, occur within the region from which Schomburgk collected the series of specimens that served as the basis of the original description of *Prochilodus insignis*. Reference to the drawing of *P. insignis* provided by Jardine (1841:261, pl. 30) shows approximately 45 scales along the longitudinal scale row located in the position of the lateral line, a number close to the range in values for this feature in what is herein considered *S. insignis* (47 to 53 scales along the lateral line), whereas *S. taeniurus* has a considerably higher number of lateral-line scales (64 to 77). In addition, the illustrated specimen has five dark bands across each caudal-fin lobe, a number that falls within the range of caudal-fin stripes in *S. insignis* (1 to 5), whereas *S. taeniurus* has a maximum of 4 dark bands on each caudal-fin lobe. Jardine (1841:262) also indicated that the material that served as the basis for the description of *S. insignis* had 38 vertebrae, but he failed to note whether that count included the centra within the Weberian apparatus and/or the terminal centra. This uncertainty casts some doubt on the utility of the feature for diagnostic purposes. Nonetheless, the vertebral count reported by Jardine (38) is closer to those in *S. insignis*, which has 39 to 41 vertebrae, than it is to the counts in *S. taeniurus*, which has 42 or 43 vertebrae. We consequently accept the description by Jardine (1841:261–262, pl. 30) of *Prochilodus insignis* as being conspecific with the form that we herein recognize as *Semaprochilodus insignis*.

In the same publication, Jardine (1841:260, pl. 29) described *Prochilodus binotatus* from material that originated in the Rio Branco, Brazil. Subsequent authors have cited this species in their compendia of the species of prochilodontids (Günther, 1864:296; Eigenmann and Eigenmann, 1891:48; Eigenmann, 1910:424; Fowler, 1950:216), but they did not delve into the question of its validity (see below concerning use of name by Kner (1859:148)). Because of the pattern of dark bands across the caudal-fin lobes (no horizontal band on the median caudal-fin rays is shown) and the anal fin, it at first appears appropriate to assign the illustrated specimen of *Prochilodus binotatus* to *Semaprochilodus*. In his treatment of the Venezuelan species of *Semaprochilodus*, Mago-Leccia (1972:58) noted in passing that "the status of *Prochilodus* (=*Semaprochilodus*) *binotatus* Schomburgk is uncertain and it is not considered here" (our translation) but did not detail the basis for this uncertainty. Géry (1977:215) similarly remarked without elaboration that *Semaprochilodus binotatus* was "a dubious species." Although *Prochilodus binotatus* is shown to have anal-fin and caudal-fin stripes reminiscent of those of *Semaprochilodus* species, it also has a dark, circular, humeral mark accompanied by a similar mark on the caudal peduncle (see Jardine, 1841, pl. 60). No known member of the Prochilodontidae has such dark humeral and caudal peduncle pigmentation. Furthermore, Jardine (1841:260) remarked that the "teeth were thickly set in each jaw, and the tongue is stated as round and fleshy" and continued that these are "at variance with the generic characters [for *Prochilodus*] as given previously," a finding confirmed by the results of this study. Equally striking is Jardine's statement that the "intestines have no appendices" evidently referring to the lack of the pyloric caecae that occur in large numbers in members of the Prochilodontidae (see Menin and Mimura, 1993, fig. 2). Because of all of these factors, it is likely that the description and illustration of *Prochilodus binotatus* provided by Jardine represent mosaics of more than one species examined in the field by the collector, Schomburgk, perhaps with only one of these being a *Semaprochilodus* species that served as the basis for the anal-fin and caudal-fin pigmentation patterns. The available evidence, thus, renders *Prochilodus binotatus* a nomem dubium.

Prochilodus binotatus, as utilized by Kner (1859:148) for material collected by Natterer in the Rio Negro basin, Brazil, undoubtedly refers to *S. insignis,* as indicated by the scale counts reported by Kner in that publication. The use of the name *Salmo jaraqui* by Kner in the same publication (1859: 148), was, according to that author, based upon the name written by Natterer in the field notes associated with the specimens examined by Kner. This name is undoubtedly derived from the common name of "jaraqui," which is used locally for *S. insignis* in the Rio Negro system. The etymology of the name lends further support to the equivalence of *P. binotatus* and *Salmo jaraqui* of Kner (1859).

In his description of *Prochilodus theraponura,* Fowler (1906:313–316, fig. 14) suggested that the species, described on the basis of 42.6 mm SL holotype that originated in the "Ambyiacu River, Equador" (= Río Ambiyacu, Peru), "may at east provisionally be regarded as distinct." The action was based upon the presence of "but two oblique bars on the caudal aside from the median one," a count that Fowler contrasted with the higher number of oblique caudal-fin bars reported by previous authors for *Prochilodus insignis* (the *Semaprochilodus insignis* of this study). Our examination of more extensive series of specimens indicates that the number of stripes across each caudal-fin lobe within *S. insignis* ranges from 2 to 7. Comparisons of examined meristic and morphometric features Table 19), pigmentation, and details of overall head and body morphology have failed to reveal any basis on which to discriminate *S. insignis* and *Prochilodus theraponura,* and these nominal forms are herein considered to be conspecific.

In that same publication, Fowler (1906:316–318, fig. 15) proposed a second new prochilodontid species, *Prochilodus amazonensis.* The description of this species also was based olely on the holotype, which originated from an unspecified ocality in the "Lower Amazons." As in the case of *P. theraponura* discussed in the preceding paragraph, *P. amazonensis* was distinguished by Fowler from *Prochilodus insignis* (= *Semaprochilodus insignis* herein) in having "fewer blackish bars on the caudal lobes," in this case three bars on each caudal-fin lobe. Our examination of a more extensive series of specimens indicates that the number of dark stripes across each caudal-fin lobe ranges from 2 to 7, thereby encompassing the value reported by Fowler for *Prochilodus amazonensis.* This also falls within the range for *S. insignis.* Comparisons of examined meristic and morphometric features (Table 19), pigmentation, and details of overall head and body form failed to reveal any differences between *Semaprochilodus insignis* and *Prochilodus amazonensis,* and these species are herein considered to be conspecific.

MATERIAL EXAMINED.—610 specimens (114, 22.0–305.3 mm SL; partial meristic data taken on additional 43 specimens).

BRAZIL. *Amazonas:* Manaus (3°06′S, 60°00′W), BMNH 1913.7.25:2, 1 (1, 61.6); BMNH 1913.11.12:35–36, 2 (1, 42.6–54.3); BMNH 1929.11.18:8, 1 (1, 124.0); BMNH 1970.4.2:12, 1 (1, 61.6); CAS-SU 39294, 1 (1, 208.2); MZUSP 9578, 1 (191.2); USNM 119958, 7 (7, 115.0–252.3); USNM 290151, 2 (2, 191.6–204.0). Rio Negro, Lago do Aleixo, MCZ 20100, 1 (276.0). Rio Negro, MCZ 799, 3 (1, 100.5–116.3); MCZ 20158, 7 (210.2–246.0). Rio Negro, Manaus (3°06′S, 60°00′W), MCZ 808, 1 (128.8); MZUSP 5867, 2 (29.1–30.9); MZUSP 6679, 13 (101.3–149.9). Rio Negro, opposite Manaus, NRM 24735, 1; NRM 24736, 1. Vicinity of Manaus, white-water river, NRM 16812, 1; NRM 24726, 3. Rio Amazonas, Manaus (3°06′S, 60°00′W), MCZ 20134, 4 (230.0–240.0). Igarapé Mauá, Manaus, MZUSP 4626–4628, 3 (108.2–139.4). Igarapé Tarumãzinho, N of Manaus (3°08′S, 60°00′W), MZUSP 6772, 1 (211.4). Lago Januari, near Manaus (3°12′S, 60°05′W), MZUSP 6871, 1 (121.3). Camaleão, Ilha da Marchantaria (3°10′S, 59°45′W), USNM 229066, 2 (2, 69.4–74.0) [2R]. "Ressaca" on Ilha da Marchantaria (3°10′S, 59°45′W), USNM 290063, 4 (4, 60.0–67.7) [2R]; USNM 290067, 3 (3, 31.0–38.6). Beach of Ilha da Marchantaria (3°10′S, 59°45′W), USNM 290124, 190 (10, 24.3–78.0); USNM 290148, 3 (3, 61.0–117.3). Furo between Lago Murumuru and Paraná do Janauacá, USNM 290149, 8 (8, 63.0–87.0). Paraná do Janauacá, entrance to Lago do Castanho (3°28′S, 60°17′W), USNM 290064, 1 (1, 41.0). Lago Murumuru, near "curral de gado do INPA," Janauacá (3°28′S, 60°17′W), USNM 290065, 2 (2, 22.0–27.0); USNM 290066, 1 (1, 37.0); USNM 290123, 1 (1, 107.0) [1R]. Lago Janauacá and vicinity, Rio Solimões (approximately 3°28′S, 60°17′W), MZUSP 21700, 1 (118.3). Rio Amazonas, Parintins (2°36′S, 56°44′W), MCZ 20056, 1 (176.0); MCZ 20058, 4 (119.7–168.3); MCZ 20104, 1 (152.0); MCZ 20128, 3 (136.0–166.0); MCZ 20129, 15 (95.3–110.4) [3R]. Villa Bella (= Rio Amazonas at Parintins and environs), NRM 7071, 1. Rio Urubu, 25 mi [=45 km] from Itacoatiara (3°08′S, 58°25′W), USNM 179561, 2 (2, 102.0–163.0). Paraná do Janauari, MCZ 20064, 17 (118.8–137.7); MCZ 20066, 30 (112.1–153.3); MCZ 20157, 3 (127.0–151.0). Lago Terra Preta, Janauari, USNM 290062, 1 (1, 117.5) [1R]. Rio Solimões, Tefé (3°24′S, 64°45′W), BMNH 1897.12.1:290, 1 (1, 128.9); MCZ 20051, 14 (1, 224.2–270); MCZ 20055, 1 (1, 99.4); MCZ 20103, 4 (145.0–168.0); MNHN 09.124-125, 2 (1, 91.5–123.5). Rio Solimões, Manacapuru

(3°06′S, 61°30′W), BMNH 1925.10.28:74, 1 (1, 213.2); MCZ 20147, 5 (95.7–119.1); USNM 162817, 1 (1, 123.0). Lago Jacaré, upriver of Manacapuru (approximately 3°06′S, 61°30′W), MZUSP 6455, 4 (138.0–144.3). Fonte Boa (2°03′S, 66°01′W), MCZ 20073, 1 (105.4); MCZ 20106, 1 (133.2). Igarapé Tomé, Auati-Paraná, NW of Fonte Boa (approximately 2°03′S, 66°01′W), MZUSP 20981, 1 (200.4). Itacoatiara, MCZ 20050, 3 (114.3–131.1); MZUSP 13493–96, 4 (184.0–209.7). Lago Curuçá, below Itacoatiara, MZUSP 13549–13550, 2 (302.5–305.3). Rio Tonantins, Tonantins (2°47′S, 67°47′W), MCZ 20067, 1 (125.0); MCZ 20069, 1 (127.6); MNHN 09.245–246, 2 (1, 106.3–107.2). Tabatinga (4°14′S, 69°44′W), MCZ 20084, 1 (126.4); MNHN 09.175, 1 (1, 120.0). Rio Madeira, Maués, MCZ 20075, 4 (232.0–260.0); USNM 119956, 1 (1, 235.2). Jatuarana, MCZ 20089, 4 (221.0–260.0); UMMZ 14552, 2 (1, 242.0–247.5). Mouth of Rio Pacia, MZUSP 21482, 2 (252.1–265.9). Codajás, MCZ 20153, 17 (109.6–119.9). Lago Saraçá, Silves, MCZ 20049, 5 (92.9–118.7). Rio Canumã (4°02′S, 59°04′W), MZUSP 7052, 15 (124.7–197.0). Lago Beruri, Rio Purus (3°52′S, 61°20′W), MZUSP 6000, 1 (1, 275.4). Rio Içá, border between Brazil and Bolívia (3°07′S, 67°58′W), MCZ 20113, 4 (111.3–116.4). Lago Coari, Coari (4°05′S, 63°08′W), MCZ 20062, 1 (1, 205.0). *Pará:* Lago Arari, MZUSP 3587, 24 (88.7–161.2). Rio Tapajós, MCZ 20163, 2 (171.0–172.0). Rio Tapajós, Santarém (2°26′S, 54°42′W), CAS 58890, 4 (4, 69.1–83.1); CAS 58894, 6 (6, 71.7–87.9) [3R]; CAS 58979, 1 (1, 63.4); CAS 58981, 1 (1, 79.5). Santarém (2°26′S, 54°42′W), BMNH 1856.3.25:17–18, 2 (1, 80.9–82.6); CAS 58884, 3 (3, 90.8–109.0) [3R]; MCZ 19824, 2 (69.4–70.6); MCZ 20080, 1 (95.4); MCZ 20124, 2 (112.0–133.0); MCZ 20227, 2 (100.9–110.7); MNHN 09.62–61, 2 (1, 200.2–203.9); USNM 119957, 3 (3, 200.0–224.4). Rio Maicá, Santarém (2°26′S, 54°42′W), MZUSP 9174, 10 (99.9–123.3). Lago Maicá, Santarém (2°26′S, 54°42′W), CAS 58983, 1 (1, 195.9). Rio Trombetas, Oriximiná (1°45′S, 55°32′W), MZUSP 8249, 1 (1, 124.2). Lago Jacupá, Oriximiná (1°45′S, 55°32′W), MZUSP 5515, 8 (225.2–273.2). Lago Paru, Oriximiná (1°45′S, 55°32′W), MZUSP 5598, 1 (192.5). Lago Paranacuí, Oriximiná (1°45′S, 55°32′W), MZUSP 5577, 1 (292.1). Óbidos (1°52′S, 55°30′W), MCZ 20114, 1 (151.0); MCZ 20137, 3 (95.0–129.5); MCZ 20138, 2 (131.3–142.1). Porto de Mós, Rio Xingú, MCZ 20110, 2 (89.0–91.0). Porto Flexal, Rio Tapajós, MZUSP 25300, 2 (273.9–300.0). Lago Jacaré, Rio Trombetas, MZUSP 4620–4622, 3 (248.1–261.4). Lago Grande, CAS 58984, 1 (1, 148.6). *Rondônia:* Praia de Paraíso, Rio Machado (approximately 8°30′S, 62°30′W), MZUSP 14016, 6 (191.4–220.5). *Roraima:* Paraná Mararå, Rio Branco, MZUSP 29256, 1 (1, 220.3) [1R]; MZUSP 29260, 1 (215.6) [1R]. *Inexact Locality:* Amazonas and Pará, MZUSP 3298, 1 (1, 136.7); MZUSP 21422, 4 (99.4–124.1); MZUSP 21423, 4 (107.5–144.1).

COLOMBIA. *Amazonas:* Río Amazonas, Leticia (4°09′S, 69°57′W), ANSP 135997, 1 (1, 71.0); UMMZ 191062, 1 (1, 163.8).

ECUADOR. *Napo:* Laguna Jatuncocha (1°00′S, 75°27′W), Río Napo, FMNH 97294, 1 (1, 273.4) [1R].

GUYANA. *Essequibo:* Rupununi River, Pirara Creek, BMNH 1972.7.27:427, 1 (1, 265.8).

PERU. *Loreto:* Río Nanay, upriver of Cocha Marona, near Iquitos (approximately 3°46′S, 73°15′W), ANSP 137798, 1 (1, 94.7); ANSP 137799, 1 (1, 95.6). Río Nanay, approximately 20 km upriver of its mouth (3°51′S, 73°15′W), USNM 280655, 1 (1, 85.1). Small "caño" tributary to Río Nanay, NE of Iquitos (3°49′S, 73°11′W), USNM 280654, 1 (1, 85.4). Río Nanay basin, Quebrada Sushuna, on road between Quistacocha and Puerto Almendra, 16 km from Iquitors, NRM 30712, 7. Río Nanay basin, Bella Vista, Vieja Cocha, NRM 30706, 2. Río Itaya, pools near Tocón Grande at km 33 on road between Iquitos and Nauta, NRM 30680, 3. Río Itaya basin, Quedbrada Pintoyacu, where crossed by road between Iquitos and Nauta, NRM 30705, 2. Caño Moena, Iquitos (approximately 3°46′S, 73°15′W), MZUSP 15227, 2 (54.1–55.3); MZUSP 15228, 1 (1, 53.9). Río Ampiyacu, near Pebas (Pevas, 3°20′S, 71°49′W), ANSP 8033, 1 (1, 42.6, holotype of *Prochilodus theraponura*) [1R]; CAS-SU 36625, 1 (66.2). Río Ampiyacu (3°20′S, 71°49′W), USNM 175856, 1 (1, 179.0). Caño Shansho (near Pebas, approximately 3°20′S, 71°49′W), CAS-SU 60518, 1 (70.9). Caño Pevas (3°20′S, 71°49′W), USNM 175853, 1 (1, 91.7). Caño Tuyé, CAS-SU 59440, 1 (1, 89.8) [1R]; USNM 175854, 1 (1, 101.2). Cocha Tuyé, CAS-SU 36624, 1 (1, 74.6); CAS-SU 60736, 1 (1, 72.4) [1R]; USNM 175855, 2 (2, 99.5–109.7). Mouth of Río Samiria, BMNH 1977.3.10:174, 1 (1, 137.1) [1R]. Contamana, Río Ucayali (7°02′S, 74°14′W), ANSP 86873, 1 (1, 93.8). Boca Chica, Río Ucayali basin, ANSP 73183, 3 (3, 72.0–91.2). Río Napo basin, Cayapoza, NRM 30686, 1. *Inexact Locality:* Lower portion of Río Amazonas basin, ANSP 21350, 1 (1, 89.5, holotype of *Prochilodus amazonensis*) [1R].

Semaprochilodus kneri (Pellegrin, 1909)

FIGURES 61, 67; TABLE 20

Prochilodus kneri Pellegrin, 1909b:155 [type locality: Orénoque (=Venezuela, Río Orinoco)].—Bertin, 1947:36 [type depository].—Mago-Leccia, 1970:21 [Venezuela].

Semaprochilodus kneri.—Mago-Leccia, 1972:61, fig. 9 [redescription; Río Orinoco basin]; 1978:11 [Venezuela].—Géry, 1977:215 [Río Orinoco].—Novoa R. et al., 1982:277 [Venezuela, Río Orinoco; common name; life history; fisheries].—Géry and Mahnert, 1984:172 [as possible junior synonym of *Semaprochilodus theraponura*, Fowler, 1906].—Lowe-McConnell, 1984:143 [economic importance].—Machado-Allison et al., 1987:134 [occurrence in llanos (savannahs) of Venezuela; natural history].—Castro, 1988:504 [comparison with *Semaprochilodus varii*].—Lasso, 1988:133 [lower Río Orinoco]; 1992:15 [Venezuela, Río Suapure; ecology].—Lasso et al., 1990:141 [Venezuela, Lago de Guri].—Taphorn and García Tenia, 1991, fig. 3 [Venezuela, Río Caroni basin, Río Claro].—Taphorn, 1992:487 [Venezuela, Río Apure basin; life history].—Taphorn et al., 1997:79 [Venezuela].—Winemiller and Jepsen, 1998:285 [Venezuela, Río Cinaurco; feeding and spawning migrations; predation by *Cichla*].—Machado-Allison et al., 1999:66 [Venezuela, Río Caura basin].—Ponte J. et al., 1999:42 [Venezuela, delta of Río Orinoco].

Semaprochilodus knerii.—Menezes and Vazzoler, 1992:63 [reproductive characteristics; species name misspelled].

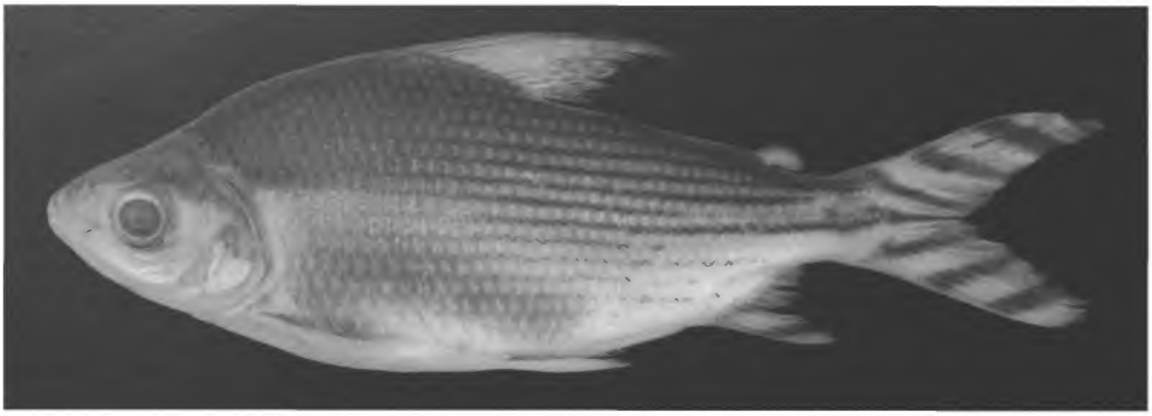


FIGURE 67.—*Semaprochilodus kneri,* ANSP 158852, 119.5 mm SL; Venezuela, Bolivar, caño crossing road to Las Trincheras, 2.7 km south of intersection with highway between Ciudad Bolivar and Caicara.

DIAGNOSIS.—*Semaprochilodus kneri* is distinguished from *S. brama, S. laticeps,* and *S. varii* by its lack of the very dark pigmentation on the membranous border of the opercle and on the exposed lateral surface of the pectoral girdle that occurs in those three species and by the possession of 40 to 42 vertebrae in contrast to the 35 to 37 vertebrae in the assemblage formed by those three species. *Semaprochilodus kneri* can be readily discriminated from *S. taeniurus* in the number of scales along the lateral line (45 to 49 versus 64 to 77, respectively), the number of horizontal rows of scales between the dorsal-fin origin and the lateral line (8 or 9 versus 12 to 14, respectively), and the number of horizontal rows of scales around the caudal peduncle (16 to 20 versus 23 to 26, respectively). Finally, *Semaprochilodus kneri,* which is distributed through the Río Orinoco basin, differs from *S. insignis,* which is endemic to the Amazon basin, in the number of horizontal rows of scales between the pelvic-fin insertion and the lateral line (7 to 9 with 9 in only 7.9% of the 38 specimens examined for this feature, versus 9 to 11, 10 most frequent, with 9 scales in only 23.5% of examined specimens, respectively; Figure 65), the number of horizontal rows of scales between the anal-fin origin and the lateral line (6 or 7, 6 most frequent with 7 in 21% of the 38 specimens examined for this feature, versus 7 to 9, 8 most frequent, respectively; Figure 63), the number of horizontal scale rows from the dorsal-fin origin to the lateral line (8 or 9, 8 most frequent and 9 in only 21.0% of the 38 specimens examined for this feature, versus 9 to 11, 10 most frequent and 9 in only 16% of the 150 specimens examined for this feature, respectively; Figure 64), the range and mode of the number of lateral-line scales (45 to 49, 47 most frequent and 48 and 49 in only 18.9% of specimens examined for this feature, versus 47 to 53, 48 most frequent and 49 frequent, respectively; Figure 66), and the form of the vertically expanded articular surface of the uncinate process of the second epibranchial (subdivided versus continuous).

DESCRIPTION.—Morphometric and meristic data for *Semaprochilodus kneri* presented in Table 20. Body moderately high and laterally compressed. Greatest body depth at dorsal-fin origin. Dorsal profile of head slightly concave. Predorsal profile of body moderately convex. Dorsal profile of body posteroventrally inclined along dorsal-fin base; slightly convex to straight from posterior of dorsal-fin base to adipose-fin origin and concave along caudal peduncle. Predorsal region of body with slight median ridge. Postdorsal region of body obtusely rounded transversely. Ventral profile of body moderately convex from tip of lower jaw to posterior of anal-fin base, and concave along caudal peduncle. Prepelvic region transversely flattened immediately anterior to pelvic-fin insertion. Slightly developed median keel extending between pelvic-fin insertion and anus.

Head profile pointed. Mouth terminal. Snout length greater than horizontal width of orbit. Nares of each side of head close to each other; anterior nares circular, posterior nares crescent shaped. Adipose eyelid present and more developed anteriorly, but with most of eye uncovered. Lips fleshy, less developed than in *Ichthyoelephas* and *Prochilodus,* but forming oral disk when protracted.

Functional teeth in two rows in each jaw. All teeth movably implanted in flesh that overlies jaws. All teeth of similar size, with exposed portions spoon shaped except when worn down. Inner tooth series in each jaw with 10 to 14 teeth on left side of upper jaw and 4 to 9 teeth on left side of lower jaw. Outer row of teeth in each jaw with approximately 100 teeth on each side of upper jaw and approximately 80 teeth on each side of lower jaw of lectotype. Upper and lower lips bordered by numerous globular, fleshy papillae.

Scales cycloid. Scales in middorsal series between posterior of dorsal-fin base and adipose-fin origin similar in form to other scales of body, but with spatulate, well-developed membranous process along posterior margin of each scale in that se-

TABLE 20.—Morphometrics and meristics of *Semaprochilodus kneri:* (A) lectotype of *Prochilodus kneri,* MNHN 1887-708; (B) paralectotypes of *Prochilodus kneri,* MNHN 1887-709–710; and (C) all specimens of *Semaprochilodus kneri* from which counts and measurements were taken. Standard length is presented in mm; values 2 to 16 are percentages of SL, 17 to 21 are percentages of HL.

Characters	A	B	C
		Morphometrics	
1. Standard length	204.9	87.6–152.7	70.0–282.4
2. Greatest body depth	36.7	38.8–39.6	31.3–43.4
3. Predorsal length	44.7	45.8–46.6	40.2–51.4
4. Dorsal-fin base length	18.2	17.4–17.4	14.2–20.9
5. Dorsal fin to adipose fin distance	25.3	26.6–28.2	17.9–29.9
6. Dorsal fin to caudal fin distance	43.1	43.5–45.3	41.0–47.1
7. Prepelvic length	55.4	51.4–53.0	47.6–56.2
8. Preanal distance	80.1	74.5–76.8	70.0–83.3
9. Snout to anal-fin insertion	85.3	80.1–80.6	73.2–88.7
10. Anal-fin base length	9.1	9.2–10.2	8.8–15.9
11. Caudal-peduncle length	13.1	13.2–14.0	11.1–14.9
12. Dorsal-fin length	35.7	27.7–39.0	27.7–52.9
13. Pectoral-fin length	19.8	17.8–18.6	17.8–21.7
14. Pelvic-fin length	20.5	16.9–22.6	16.9–22.9
15. Least caudal-peduncle height	11.1	10.6–11.1	9.5–11.5
16. Head length	28.6	28.6–29.1	26.3–32.9
17. Snout length	32.9	31.0–32.8	31.0–40.0
18. Bony orbital diameter	25.6	27.5–28.2	22.2–35.0
19. Postorbital length	41.0	40.8–41.3	34.1–42.9
20. Interorbital width	45.9	46.7–48.9	42.6–53.0
21. Mouth width	37.5	38.0–39.7	37.5–45.6
		Meristics	
Lateral-line scales	49	47–48	45–49
Scale rows between dorsal-fin origin and lateral line	9	8	8–9
Scale rows between anal-fin origin and lateral line	6	6	6–7
Scale rows between pelvic-fin insertion and lateral line	8	8	7–9
Rows of scales around caudal peduncle	19	16–19	16–20
Median predorsal scales	14	12–13	11–15
Median scales between dorsal and adipose fins	15	16–16	14–18
Vertebrae	41	41–42	40–42
Inner row teeth, upper jaw	14	10	10–14
Inner row teeth, lower jaw	7	4–7	4–9

ries. Lateral line with 45 to 49 (48.6% of specimens with 47) pored scales; 8 or 9 (78.9% of specimens with 8) horizontal rows of scales between dorsal-fin origin and lateral line; 7 to 9 (73.7 % of specimens with 8) horizontal rows of scales between pelvic-fin insertion and lateral line; 6 or 7 (78.9% of specimens with 6) horizontal rows of scales between anal-fin origin and lateral line; 11 to 15 (47.4% of specimens with 13) median predorsal scales; 14 to 18 (40.5% of specimens with 15) scales in middorsal series between posterior of dorsal-fin base and adipose-fin origin; 16 to 20 (26.3% of specimens with 16) horizontal rows of scales around caudal peduncle.

Vertebrae 40 to 42 (69.7% of specimens with 41).

Dorsal fin preceded by small, but well-developed, anteroventrally bifurcate, procumbent spine somewhat triangular in lateral view. Dorsal-fin rays (including procumbent spine) iii,9 or 10 (iii,10 most frequent) [iii,10]; anal-fin rays iii,7 to 9 (iii,8 most frequent) [iii,8]; pectoral-fin rays i,12 to 15 (i,15 most frequent) [i,15]; pelvic-fin rays i,7 or 8 (i,8 most frequent) [i,8]; principal caudal-fin rays 10/9 [10/9].

Dorsal fin distally pointed; posterior unbranched and anterior branched rays longest and subequal. Dorsal-fin origin located closer to tip of snout than to caudal-fin base. Greatest length of adipose fin approximately equal to three-fourths of horizontal width of orbit. Adipose-fin origin located along vertical that passes through middle of anal-fin base. Pectoral fin distally pointed. Tip of adpressed pectoral fin extending posteriorly to, or almost to, pelvic-fin insertion. Pelvic fin falcate. Pelvic-fin insertion located slightly posterior of vertical that passes through dorsal-fin origin. Tip of adpressed pelvic fin reaching posteriorly approximately two-thirds of distance between pelvic-fin insertion and anus. Axillary scale present, length approximately one-half of length of pelvic fin. Posterior unbranched and anterior branched rays of anal fin longest and subequal. Caudal fin bifurcate.

COLORATION IN ALCOHOL.—Ground coloration silvery golden, with middorsal portion of body and head darker. Approximately 12 dark, wavy, horizontal stripes on side of body; stripes formed by concentrations of dark melanophores along dorsal and ventral exposed margins of scales. Approximately 2 to 6 [5] wavy stripes dorsal to, and 3 to 6 [3] wavy stripes ventral to, lateral line; stripes less uniform on caudal peduncle. Diffuse field of brown chromatophores on membranous portion of opercle and on exposed lateral surface of pectoral girdle.

Dorsal fin with 1 to 4 (3 most frequent) [4] irregular dark stripes beginning on anterior margin of fin and extending across fin approximately parallel to fin base. Adipose fin with distinctly dark dorsal border. Pectoral and pelvic fins hyaline. Anal fin hyaline overall, with patches of dark chromatophores forming 3 or 4 (most frequently 3) [4] irregular oblique stripes; stripes extending across fin, with anterior bands running in parallel; stripes absent in some rare individuals. Caudal fin with 7 to 9 (most frequently 9) [8] dark bands. Horizontal stripe overlying middle caudal-fin rays; caudal fin with 3 or 4 (most frequently 4) [4] oblique bands on dorsal lobe and 3 or 4 (most frequently 4) [3] oblique stripes on lower lobe. Iris silvery golden, with diffuse darker regions on dorsal and ventral portions.

DISTRIBUTION.—*Semaprochilodus kneri* is only known to occur in the Río Orinoco basin (Figure 61, dots).

COMMON NAME.—Bocachico del Orinoco (Venezuela).

COMPARISONS.—*Semaprochilodus kneri* was redescribed in detail by Mago-Leccia (1972:61–64, fig. 9) who concluded that it is a valid species endemic to the Río Orinoco basin. *Semaprochilodus kneri* differs from *S. insignis* in four meristic characters for which the modal values of the two forms are shifted significantly (See Figures 63–66), with varying, sometimes minimal degrees, of overlap in the ranges for a particular feature between the two species. *Semaprochilodus kneri* also differs from *S. insignis* in the form of the vertically expanded articular surface of the uncinate process of the second epibranchial (see description of character under "Second Epibranchial," above). Furthermore, the known distributional ranges of *S. kneri* and *S. insignis* are completely allopatric in the Río Orinoco and Rio Amazonas basins, respectively. We consequently consider the *Semaprochilodus kneri* and *S. insignis* to be distinct species despite their similarity in external morphology.

REMARKS.—Pellegrin (1909b:155–156) based his description of *Prochilodus kneri* upon three specimens collected by Chaffanjon in the Río Orinoco, Venezuela. We herein designate the largest syntype (MNHN 1887-708, 204.9 mm SL), which is also in the best condition, as the lectotype, and the two other specimens in the series (MNHN 1887-710, 87.6 mm SL; MNHN 1887-709, 152.7 mm SL), thus, become paralectotypes.

MATERIAL EXAMINED.—210 specimens (39, 70.0–282.4 mm SL).

VENEZUELA. *Amazonas:* Caño crossing road between Puerto Ayacucho and El Burro, approximately 7 km from intersection with road between Puerto Ayacucho and Caicara, ANSP 158851, 11 (1, 106.9–282.4). Confluence of caño Orera with Río Orinoco, approximately 15 minutes upriver of El Burro, ANSP 158864, 31 (2, 82.3–140.5). Caño 28.3 km SW of El Burro, on road between Caicara and Puerto Ayacucho, ANSP 158861, 12 (2, 96.5–116.2). Morichal (palm swamp) 26.9 km from Puerto Ayacucho, on road between Caicara and Puerto Ayacucho, ANSP 158859, 9 (2, 89.0–119.6) [9R]. Río Autana, approximately 8.0 km upriver of its confluence with Río Sipapo, ANSP 158862, 1 (1, 222.2). Departamento de Ature, Balneiria Pozo Azul, approximately 30 km N of Puerto Ayacucho (5°53′N, 67°28′W), USNM 270325, 1 (1, 99.3) [1R]. Río Atabapo, approximately 5.0 km upriver of its mouth, San Fernando de Atabapo, LIRP 1308, 1 (1, 220.0). *Bolivar:* Caño Quiribana, in Caicara, CAS-SU 54589, 5 (5, 100.8–113.5). Caño Quiribana, CAS-SU 56805, 1 (1, 113.5) [1R]; CAS-SU 56810, 1 (1, 103.9) [1R]. Confluence of caño Quiribana with Río Orinoco, CAS-SU 54707, 1 (1, 24.2) [1R]. Caño Caiman where crossed by road between Caicara and Puerto Ayacucho, 19.2 km W of intersection with road between Ciudad Bolivar and Caicara, ANSP 158869, 2 (1, 105.9–107.0). Small caño where crossed by road between Caicara and Puerto Ayacucho, 18 km N of Manipure, ANSP 158860, 13 (1, 86.7–102.9). Río and flooded area 15 km N of Manipure, on road between Caicara and Puerto Ayacucho, ANSP 158858, 19 (1, 93.7–135.0). Río Urbana (Urbani), on road between Maripas and Las Trincheras, ANSP 135782, 2 (1, 95.4–107.6). Caño where crossed by road to Las Trincheras, 2.7 km S of intersection with road between Ciudad Bolivar and Caicara, ANSP 158852, 37 (1, 97.9–144.9). Río Agua Blanca, 100 to 600 m below bridge on road between Caicara and Ciudad Bolivar, ANSP 158855, 19 (1, 77.7–112.2). Small caño tributary to Río Caura, 15 minutes below hydroelectric plant on Río Caura, ANSP 135918, 2 (1, 101.2–105.7). Backwater of Río Nichare, approximately 10 minutes from confluence of Ríos Nichare and Caura, ANSP 139570, 23 (2, 98.9–172.1). Small caño tributary to Río Mato, ANSP 139868, 9 (2, 91.9–114.4). Small caño connecting with Río Orinoco immediately S of El Burro (6°11′N, 67°25′W), USNM 295332, 1 (1, 70.0) [1R]. *Guárico:* Río Guariquito, government reserve E-SE of Calabozo (8°35′N, 67°15′W), USNM 257560, 5 (5, 140.6–165.7) [5R]. *Inexact Locality:* Orénoque (=Río Orinoco), MNHN 1887-708, 1 (1, 204.9, lectotype of *Prochilodus kneri*) [1R]; MNHN 1887-709, 1 (1, 152.7, paralectotype of *Prochilodus kneri*) [1R]; MNHN 1887-710, 1 (1, 87.6, paralectotype of *Prochilodus kneri*) [1R].

***Semaprochilodus laticeps* (Steindachner, 1879)**

FIGURES 68, 69; TABLE 21

Prochilodus laticeps Steindachner, 1879d:152 [type locality: Orinoco bei Ciudad Bolivar (=Venezuela, Bolivar, Río Orinoco at Ciudad Bolivar), designated by Steindachner, 1879e:152]; 1879e:152 [page 4 of separate] [more extensive species description and designation of specific type locality].—Eigenmann and Eigenmann, 1891:48 [in listing of South American fishes].—Eigenmann, 1910:424 [in listing of South American fishes]; 1912:67 [Río Orinoco basin]; 1922:231 [cited as being allied to *Prochilodus mariae*].—Schultz, 1944:262 [in part, not possible synonymies of *P. brama* and *P. kneri* into *S. laticeps*].—Luengo, 1963:336 [report of introduction of species into Lago de Valencia, Venezuela].—Fernández-Yépez, 1969:39 [Venezuela, Río Caroni].—Mago-Leccia, 1970:21 [Venezuela].—Fowler, 1975:359 [literature compilation].—Machado-Allison, 1992:46 [larval ecology, Río Orinoco basin].—Machado-Allison et al., 1999:66 [Venezuela, Río Caura basin].—Ponte J. et al., 1999:42 [Venezuela, delta of Río Orinoco].

Semaprochilodus laticeps.—Mago-Leccia, 1972:64, figs. 5d, 10 [redescription; Río Orinoco basin].—Cala, 1977:4 [Colombia, eastern llanos, Ríos Inírida and Meta].—Géry, 1977:215 [Río Orinoco].—Mago-Leccia, 1978:15 [Venezuela].—Novoa R. et al., 1982:278 [Venezuela, Río Orinoco; common name; life history; fisheries].—Lowe-McConnell, 1984:143 [in part, economic importance, not cited occurrence of species in central Amazon].—Petrere, 1985:6 [importance in Amazonian fisheries].—Castro, 1988:504 [compared with *Semaprochilodus varii*].—Menezes and Vazzoler, 1992:63 [reproductive characteristics].—Balbás and Taphorn, 1996:78 [Venezuela, Río Caura].—Taphorn et al., 1997:79 [Venezuela].—Winemiller and Jepsen, 1998:285 [Venezuela, Río Cinaurco; feeding and spawning migrations; predation by *Cichla*].—Instituto Alexander von Humboldt, 2000:184 [Colombia, Río Orinoco basin, vulnerability for local extinction].

Semaprochilodus theraponura.—Sánchez-V et al., 1999:569 [Colombia, Departamento de Meta, Rio Yucao; likely misidentification of *S. laticeps*].

DIAGNOSIS.—*Semaprochilodus laticeps* is distinguished from *S. insignis, S. kneri,* and *S. taeniurus* by its possession of intense black pigmentation on the membranous border of the opercle and on the exposed lateral surfaces of the pectoral girdle, whereas such intense pigmentation is absent in the latter three species. Among the *Semaprochilodus* species in which such dark pigmentation on the opercle and pectoral girdle is absent, *S. laticeps* differs from *S. brama* in the number of horizontal rows of scales between the anal-fin origin and the lateral line (8 or 9 versus 10 to 12) and less discretely in the number of scales along the lateral line (48 to 56, 51 most common and 56 in only 2 of the 27 specimens examined for this feature, versus 56 to 68, 58 most common and 56 in 4 of the 26 specimens ex-

FIGURE 68.—*Semaprochilodus laticeps*, USNM 233611, 101.0 mm SL; Venezuela, Monagas, Caño Guargapo.

amined for this feature, respectively). Finally, *Semaprochilodus laticeps* is readily distinguishable from *S. varii* in the number of scales along the lateral line (48 to 56 versus 39 to 41, respectively) and in the number of horizontal rows of scales between the dorsal-fin origin and the lateral line (10 or 11 versus 8).

DESCRIPTION.—Morphometric and meristic data for *Semaprochilodus laticeps* presented in Table 21. Body high and laterally compressed. Greatest body depth at dorsal-fin origin. Dorsal profile of head concave. Predorsal profile of body convex. Body profile distinctly posteroventrally inclined along dorsal-fin base; profile ranging from slightly convex to straight from posterior of dorsal-fin base to adipose-fin origin, and concave along caudal peduncle. Predorsal portion of body with median ridge. Postdorsal portion of body obtusely rounded transversely. Ventral profile of body distinctly convex from tip of lower jaw to posterior of anal-fin base. Ventral profile of caudal peduncle concave. Prepelvic region transversely flattened proximate to pelvic-fin insertion. Distinct ventral keel present between pelvic-fin insertion and anus.

Head profile pointed. Mouth terminal. Snout length equal to, or slightly greater than, horizontal width of orbit. Nares of each side of head close to each other; anterior nares circular, posterior nares crescent shaped. Adipose eyelid present but poorly developed; most pronounced anteriorly, but with much of eye uncovered. Lips fleshy, less developed than in *Ichthyoelephas* and *Prochilodus* species, and forming oral disk when protracted.

Functional teeth in two rows in each jaw. All teeth movably implanted in flesh that overlies jaws. All teeth of similar size, with exposed portions spoon shaped except when worn down. Inner tooth series in each jaw with 9 to 13 teeth on left side of upper jaw and 6 to 10 teeth on left side of lower jaw. Outer row of teeth in each jaw with approximately 67 teeth on each side of upper jaw and approximately 47 teeth on each side of lower jaw in photographed specimen. Upper and lower lips bordered by numerous globular, fleshy papillae.

Scales cycloid. Scales in middorsal series between posterior of dorsal-fin base and adipose-fin origin similar in form to those of adjoining regions of body, but with membranous spatulate process relatively well developed along posterior margin of each scale in that series. Lateral line with 48 to 56 (25.9% of specimens with 51 and 53) pored scales (approximately 53 scales reported for holotype by Steindachner (1879d)); 10 or 11 (81.5% of specimens with 10) horizontal rows of scales between dorsal-fin origin and lateral line (10 or 11 reported for holotype by Steindachner (1879d)); 9 to 12 (46.1% of specimens with 10) horizontal rows of scales between pelvic-fin insertion and lateral line (10 reported for holotype by Steindachner (1879d)); 8 or 9 (77.8% of specimens with 9) horizontal rows of scales between anal-fin origin and lateral line; 11 to 15 (30.8% of specimens with 13 to 15) median predorsal scales; 12 to 17 (48% of specimens with 15) scales in middorsal series between posterior of dorsal-fin base and adipose-fin origin; 19 to 24 (29.6% of specimens with 22 and 23) horizontal rows of scales around caudal peduncle.

Vertebrae 35 to 37 (58.8% of specimens with 36).

Dorsal fin preceded by small, but well-developed, anteroventrally bifurcate, procumbent spine somewhat triangular in lateral view. Dorsal-fin rays (including procumbent spine) iii,10 (11 rays reported for holotype by Steindachner (1879d), a count that presumably included both branched and unbranched rays); anal-fin rays iii,8 (iii,9 reported for holotype by Steindachner

TABLE 21.—Morphometrics and meristics of all specimens of *Semaprochilodus laticeps* from which counts and measurements were taken. Standard length is presented in mm; values 2 to 16 are percentages of SL, 17 to 21 are percentages of HL.

Characters	Morphometrics
1. Standard length	55.4–437.9
2. Greatest body depth	41.1–50.3
3. Predorsal length	47.3–55.9
4. Dorsal-fin base length	18.5–22.4
5. Dorsal fin to adipose fin distance	19.7–26.4
6. Dorsal fin to caudal fin distance	38.3–42.5
7. Prepelvic length	50.5–56.0
8. Preanal distance	76.7–79.8
9. Snout to anal-fin insertion	80.2–84.4
10. Anal-fin base length	11.2–13.5
11. Caudal-peduncle length	9.5–16.3
12. Dorsal-fin length	28.9–43.9
13. Pectoral-fin length	15.9–26.4
14. Pelvic-fin length	17.6–30.8
15. Least caudal-peduncle height	11.9–15.6
16. Head length	29.5–34.7
17. Snout length	32.3–41.6
18. Bony orbital diameter	17.3–37.8
19. Postorbital length	33.9–45.6
20. Interorbital width	41.0–59.3
21. Mouth width	41.5–48.6
	Meristics
Lateral-line scales	48–56
Scale rows between dorsal-fin origin and lateral line	10–11
Scale rows between anal-fin origin and lateral line	8–9
Scale rows between pelvic-fin insertion and lateral line	9–12
Rows of scales around caudal peduncle	19–24
Median predorsal scales	11–15
Median scales between dorsal and adipose fins	12–17
Vertebrae	35–37
Inner row teeth, upper jaw	9–13
Inner row teeth, lower jaw	6–10

(1879d); count may include the two ultimate branched rays that articulate with single proximal pterygiophore as separate elements contrary to practice in this study); pectoral-fin rays i,13 to 16 (i,15 most frequent); pelvic-fin rays i,8 (10 rays reported for holotype by Steindachner (1879d)); principal caudal-fin rays 10/9.

Dorsal fin distally elongate; posterior unbranched and anterior branched rays longest and subequal. Dorsal-fin origin located closer to tip of snout than to caudal-fin base. Greatest length of adipose fin approximately two-thirds of horizontal width of orbit. Adipose-fin origin located along vertical that passes through middle of anal-fin base. Pectoral fin pointed distally. Tip of pectoral fin reaching, or almost reaching, pelvic-fin insertion. Pelvic fin falcate. Pelvic-fin insertion located slightly posterior to vertical that passes through dorsal-fin origin. Tip of adpressed pelvic fin reaching posteriorly approximately three-fourths of distance between pelvic-fin insertion and anus. Axillary scale present, its length approximately one-fourth of greatest length of pelvic-fin. Posterior unbranched and anterior branched anal-fin rays longest and subequal. Caudal fin moderately bifurcate.

COLORATION IN ALCOHOL.—Ground coloration silvery yellow or yellowish brown, with dorsal portions of head and body darker. Occasional specimens with wavy, dark, horizontal stripe on lateral surface of body. Stripe accompanied by numerous indefinite and irregular spots on lateral surface of body, with number of spots greater dorsal to lateral line. Spots and stripe formed by concentrations of dark chromatophores on dorsal and ventral sections of exposed portions of scales. Dense field of brown or black chromatophores forming well-defined dark area on membranous portion of opercle and on lateral exposed surface of pectoral girdle.

Dorsal fin with 3 or 4 (most frequently 4) dark, irregular stripes beginning on anterior margin of fin and extending across fin approximately parallel to base of fin. Adipose fin outlined with dark pigmentation dorsally, with posterodorsal border black. Pectoral and pelvic fins dusky. Anal fin hyaline overall, with fields of chromatophores forming 1 to 4 (most frequently 4) irregular oblique stripes with anterior stripes parallel. Some large specimens lacking distinct dark anal-fin stripes. Caudal fin with 7 to 9 (most frequently 9) dark stripes; 1 horizontal stripe overlying central caudal-fin rays, 3 or 4 (most frequently 4) oblique stripes on upper, and 3 or 4 (most frequently 4) oblique stripes on lower, caudal lobe. Larger and presumably older specimens with pattern of dark stripes on caudal and anal fins often less obvious, occasionally to point of being apparently absent. Iris yellowish brown, with diffuse dark areas on dorsal and ventral portions.

COLORATION IN LIFE.—(Based upon a color transparency of a recently collected adult from the central portions of the Río Orinoco basin, Venezuela, taken by the second author). Dark pigmentation as described above. Ground coloration silvery; dorsal portion of body and particularly of head darker. Ground coloration of all fins light yellow, with posterior regions of anal and caudal fins reddish and much of pelvic fin intensely reddish. Iris silvery golden.

DISTRIBUTION.—*Semaprochilodus laticeps* is endemic to the Río Orinoco basin in Venezuela and Colombia (Figure 69, diamonds).

COMMON NAME.—Sapuara del Orinoco, zapoara (Venezuela).

COMPARISONS.—As noted in the "Diagnosis," above, *Semaprochilodus laticeps* can be unambiguously separated from all its congeners by various meristic and pigmentary features.

REMARKS.—The original description of *Prochilodus laticeps* by Steindachner (1879d:150; 1879e:152) was based upon a 430 mm SL specimen collected by Schilling in the Río Orinoco, in the state of Bolivar, Venezuela. We were unable to locate the holotype of the species in the holdings of the Naturhistorisches Museum Wien (NMW). Neither was it reported as extant by Eschmeyer et al. (in Eschmeyer, 1998:875), and apparently it is lost. Nonetheless, as noted by Mago-Leccia (1972:66) and confirmed by our study, the exhaustive descriptions of that nomi-

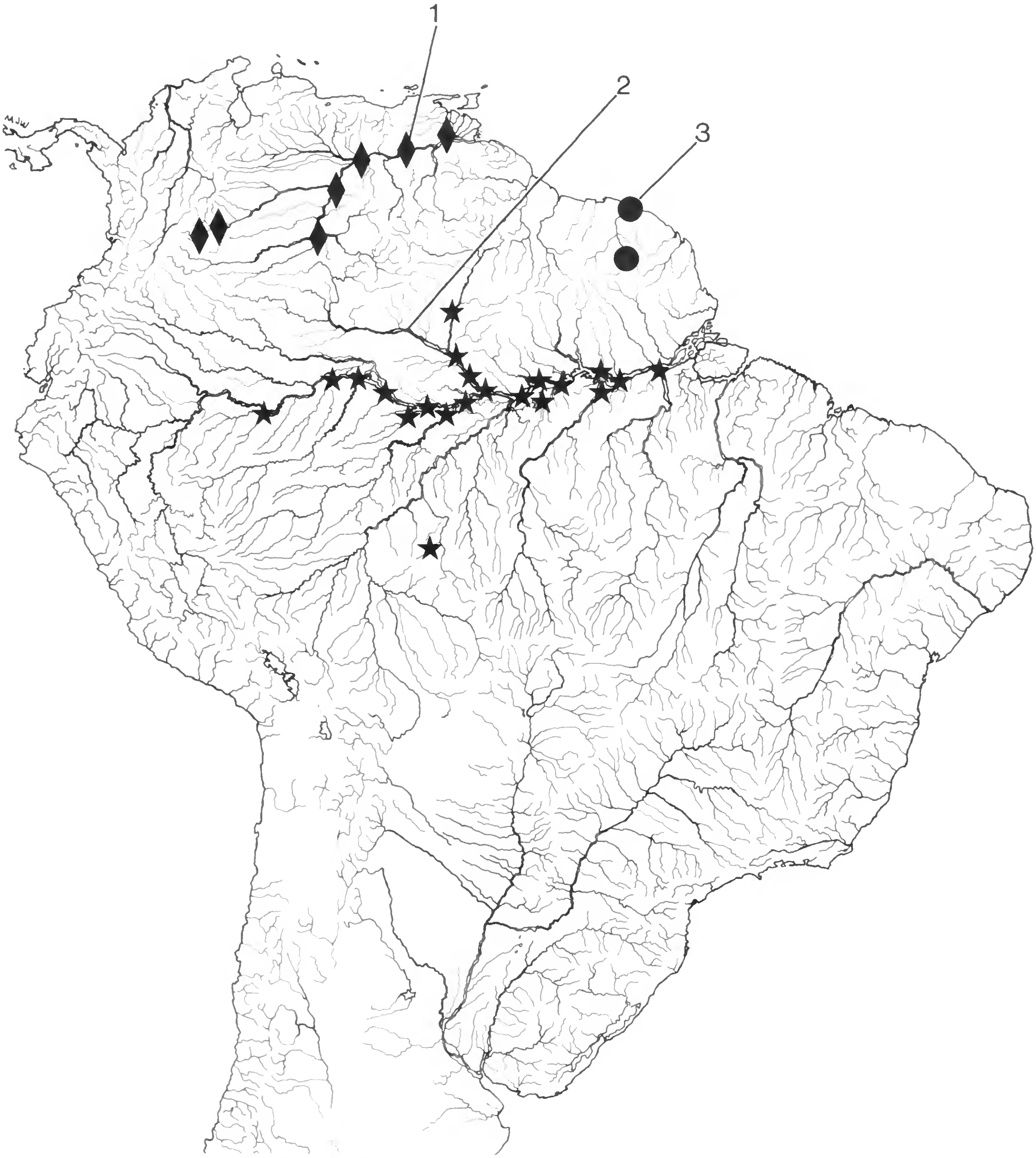


FIGURE 69.—Map of central and northern South America showing geographic distribution of *Semaprochilodus laticeps* (diamonds; 1=holotype locality), *Semaprochilodus taeniurus* (stars; 2=Rio Negro, inexact type locality), and *Semaprochilodus varii* (dots; 3=holotype locality) (some symbols represent more than one collecting locality and/or lot of specimens).

nal species provided by Steindachner (1879d:150; 1879e:152) leave no doubt as to its identity, or to its conspecificity with the material herein identified as *Semaprochilodus laticeps*.

MATERIAL EXAMINED.—38 specimens (27, 55.4–437.9 mm SL).

COLOMBIA. *Meta:* Lago Mozambique, Hacienda Mozambique, ANSP 128158, 1 (1, 437.9) [1R]. Río Manacacías, near to La Esperanza, MCZ 58973, 1 (1, 67.5)

VENEZUELA. *Amazonas:* Laguna de Titi, N of San Fernando de Atabapo, LIRP 1309, 2 (104.6–111.6). *Bolivar:* Río Orinoco, Caicara, CAS 56717, 1 (1, 130.7) [1R]; CAS 56793, 1 (1, 92.6); CAS 56813, 1 (1, 148.6) [1R]; CAS 64373, 1 (1, 194.2). 0.3 km from Puerto Nuevo in direction of Puerto Ayacucho, FMNH 85628, 16 (9, 55.4–80.9) [9R]. Small caño communicating with Río Orinoco S of El Burro (6°11'N, 67°25'W), USNM 270239, 7 (7, 75.0–89.0). *Monagas:* Caño Guargapo (8°39'24"N, 62°14'W), USNM 233080, 1 (1, 86.3); USNM 292341, 4 (4, 81.0–101.0) [4R]. Barrancas del Orinoco (8°42'S, 62°11'W), MBUCV-V-1712, 1. *Inexact Locality*: Orinoco basin, NRM 7072, 1 (125.3).

Semaprochilodus taeniurus (Valenciennes, 1817)

FIGURES 69, 70; TABLE 22

Curimatus taeniurus Valenciennes in Humboldt and Bonpland, 1817:166 [type locality: l'Amerique Equioxiale (=Equatorial America), restricted herein to Brazil, Amazonas, upper Rio Negro].—Valenciennes in Cuvier and Valenciennes, 1850:71 [shift of species to *Prochilodus*].—Taylor, 1964:261 [cited in petition to ICZN].

Anodus taeniurus.—Müller and Troschel, 1844:84 [fluvio Amazonum (=Rio Amazonas)].

Prochilodus taeniurus.—Valenciennes in Cuvier and Valenciennes, 1850:86 [based upon description in Valenciennes, 1817].—Kner, 1859:148 [comparison with *Prochilodus binotatus*].—Günther, 1864:297 [based upon Valenciennes, 1850].—Steindachner, 1881a:131 [redescription].—Eigenmann and Eigenmann, 1891:48 [in listing of South American fishes].—Eigenmann and Bean, 1907:667.—Pellegrin, 1909a:148 [Brazil: Tonantins, Santarém].—Eigenmann, 1910:424 [in listing of South American fishes].—Magalhães, 1931:128 [common name, biology].—Bertin, 1947:35 [type depository].—Fowler, 1950:225 [literature compilation]; 1975:360 [literature compilation].

Semaprochilodus taeniurus.—Mago-Leccia, 1972:58 [as recognized species of *Semaprochilodus*].—Géry, 1977:215 [middle Amazon basin].—Smith, 1981: 43 [fishing methods, relative body size].—Goulding, 1981:39 [migration patterns in middle Rio Madeira].—Junk et al., 1983:406, table 3 [Brazil, Amazon; ecology].—Lowe-McConnell, 1984:143 [economic importance].—Nomura, 1984:58 [Brazil, common name].—Araújo-Lima, 1985:430 [comparisons with other central Amazonian prochilodontids].—Ribeiro, 1985:419 [hybridization with *Semaprochilodus insignis*].—Araújo-Lima et al., 1986: 1256 [exploitation of phytoplankton].—Feldberg et al., 1986:1 [cytogenetics].—Bayley, 1988:131, table 2 [growth rates].—Castro, 1988:504 [compared with *Semaprochilodus varii*].—Vazzoler et al., 1989:165 [Brazil, Rio Negro basin; reproductive biology], 175 [Brazil, Rio Negro; spawning periods].—Ribeiro and Petrere, 1990:195 [fisheries ecology and management].—Vazzoler and Amadio, 1990:537 [schooling behavior and structure].—Menezes and Vazzoler, 1992:63 [reproductive characteristics].—Ferreira et al., 1998:40, fig. 15 [Brazil, region of Santarém; economic importance in fishery in that region].—Saint-Paul et al., 2000:239, 242 [Brazil, Amazonas, Rio Negro, Lago do Prato; abundance, occurrence in black waters].—Sánchez-Botero and Araújo-Lima, 2001:441 [Brazil, Manaus region; occurrence in aquatic macrophytes].

Semaprochilodus brama [not of Valenciennes, 1850].—Nomura, 1984:58 [Brazil, common name].

Semaprochilodus insignis [not of Jardine, 1841].—Nomura, 1984:58 [Brazil, common name].

Semaprochilodus insignis x *Semaprochilodus taeniurus*.—Ribeiro, 1985:419 [report of interspecific hybrid].

Semaprochilodus taeniatus.—Petrere, 1989:5 [economic importance at Manaus fish market; species name misspelled].

DIAGNOSIS.—*Semaprochilodus taeniurus* is distinguished from *S. brama, S. laticeps,* and *S. varii* by its lack of the intense dark pigmentation on the membranous opercular border and on the exposed surface of the pectoral girdle that occurs in those three species. *Semaprochilodus taeniurus* differs from *S. insignis* and *S. kneri,* its two congeners that similarly lack dark opercular and pectoral girdle pigmentation, in the number of scales along the lateral line (64 to 77 versus 47 to 53, and 45 to 49 scales, respectively), the number of horizontal rows of scales between the pelvic-fin insertion and the lateral line (12 to 14 versus 9 to 11, and 7 to 9, respectively), and the number of horizontal rows of scales around the caudal peduncle (23 to 26 versus 18 to 22, and 16 to 20, respectively).

DESCRIPTION.—Morphometric and meristic data for *Semaprochilodus taeniurus* presented in Table 22. Body comparatively shallow and elongate, transversely compressed. Greatest body depth at dorsal-fin origin. Dorsal profile of head gently concave to straight. Predorsal profile of body gently convex; profile posteroventrally inclined along dorsal-fin base; profile ranging from gently convex to straight from posterior of dorsal-fin base to adipose-fin origin and concave along caudal peduncle. Predorsal surface of body with very slightly developed median ridge. Postdorsal portion of body transversely obtusely rounded. Ventral profile of body gently convex from tip of lower jaw to rear of anal-fin base. Ventral profile of caudal peduncle concave. Prepelvic region of body transversely flattened proximate to pelvic-fin insertion. Well-developed median keel extending between pelvic-fin insertion and anus.

Head profile pointed. Mouth terminal. Snout length equal to, or greater than, horizontal width of orbit. Nares of each side of head close to each other; anterior nares circular, posterior nares crescent shaped. Adipose eyelid present and well developed; equally developed on anterior and posterior portions of eye and covering considerable fraction of eye. Lips fleshy, less developed than in *Prochilodus* and *Ichthyoelephas,* and forming oral disk when protracted.

Functional teeth in two rows in each jaw. All teeth movably implanted in flesh that overlies jaws. All teeth of similar size, with exposed portions spoon shaped except when worn down. Inner tooth series in each jaw with 7 to 13 teeth on left side of upper jaw and 6 to 10 teeth on left side of lower jaw. Outer row of teeth in each jaw with approximately 55 teeth on each side of upper jaw and approximately 45 teeth on each side of lower jaw in photographed specimen. Upper and lower lips bordered by numerous globular, fleshy papillae.

Scales cycloid. Scales in middorsal series between posterior of dorsal-fin base and adipose-fin origin with spatulate, well-developed, fleshy process along posterior margin of each scale in that series. Lateral line with 64 to 77 (23.1% of specimens with 69) pored scales; 12 to 14 (57.6% of specimens with 13) horizontal rows of scales between dorsal-fin origin and lateral line; 12 to 14 (54.5% of specimens with 13) horizontal rows of scales between pelvic-fin insertion and lateral line; 9 to 11 (57.6% of specimens with 10) horizontal rows of scales between anal-fin origin and lateral line; 14 to 22 (24.2% of specimens with 19) median predorsal scales; 19 to 26 (33.3% of

FIGURE 70.—*Semaprochilodus taeniurus*, MZUSP 6680, 132.2 mm SL; Brazil, Amazonas, Río Negro, Manaus.

specimens with 20) scales in middorsal series between posterior of dorsal-fin base and adipose-fin origin; 23 to 26 (78.1% of specimens with 24) horizontal rows of scales around caudal peduncle.

Dorsal fin preceded by small, but well-developed, anteroventrally bifurcate, procumbent spine somewhat triangular in lateral view. Dorsal-fin rays (including procumbent spine) iii,10 [iii,10]; anal-fin rays iii,8 [iii,8]; pectoral-fin rays i,13 to 16 (i,15 most frequent) [i,14]; pelvic-fin rays i,8 [i,8]; principal caudal-fin rays 10/9 [10/9].

Vertebrae 42 or 43 (81.2% of specimens with 42).

Dorsal fin distally pointed; posterior unbranched and anterior branched rays longest and subequal. Dorsal-fin origin located closer to tip of snout than to caudal-fin base. Greatest length of adipose fin approximately equal to two-thirds of horizontal width of eye. Adipose-fin origin located along vertical that passes through posterior one-third of anal-fin base. Pectoral fin distally pointed. Tip of adpressed pectoral fin reaching posteriorly to, or almost to, pelvic-fin insertion. Pelvic fin falcate. Pelvic-fin insertion located along vertical that passes though anterior one-fourth of dorsal-fin base. Tip of adpressed pelvic fin reaching posteriorly to area approximately one-half of distance between pelvic-fin insertion and anus. Axillary scale present, its length approximately one-third of greatest length of pelvic fin. Posterior unbranched and anterior branched anal-fin rays longest and subequal. Caudal fin bifurcate.

COLORATION IN ALCOHOL.—Ground coloration silvery yellow or yellowish brown, with dorsal portions of body and head darker. Lateral surface of body with approximately 11 to 17 dark, wavy, horizontal stripes along dorsal and ventral margins of exposed portions of scales; 6 to 8 wavy stripes dorsal to, and 2 to 5 wavy stripes ventral to, lateral line; stripes somewhat irregular on caudal peduncle. Diffuse field of brown chromatophores on membranous portion of opercle and on lateral exposed portion of pectoral girdle. Diffuse dark mark on lateral surface of opercle.

Dorsal fin with 2 or 3 (most frequently 3) irregular dark stripes beginning at anterior margin and extending across fin approximately parallel to base of fin. Anterodorsal portion of adipose fin dusky with fine black border. Pectoral and pelvic fins dusky. Anal fin hyaline with fields of dark chromatophores forming 1 to 3 (most frequently 3) (1 stripe reported for holotype by Valenciennes (1817)) irregular, oblique stripes extending across fin, with anterior stripes running in parallel. Occasional specimens lack definite anal-fin stripes. Caudal fin with 5 to 9 (most frequently 6) dark stripes (7 dark stripes reported for holotype by Valenciennes (1817)), 1 stripe overlying middle caudal-fin rays, 2 to 4 (most frequently 3) (3 dark stripes reported for holotype by Valenciennes (1817)) oblique stripes on upper lobe, and 2 to 4 (most frequently 3) (3 dark stripes reported for holotype by Valenciennes (1817)) on lower lobe of caudal fin. Iris reddish brown, with diffusely dusky area on dorsal and ventral portions.

DISTRIBUTION.—*Semaprochilodus taeniurus* is known from the central portions of Amazon basin and tributary rivers, including the Rio Negro, Rio Branco, Rio Madeira, and Rio Tapajós (Figure 69, stars), that are, with the exception of the last basin, black- and white-water rivers. This species is apparently absent from the clear-water Rio Xingú and Rio Tocantins.

COMMON NAME.—Jaraqui, jaraqui-da-escama-fina (Brazil).

Comparisons.—*Semaprochilodus taeniurus* is readily distinguished from its congeners by the meristic and pigmentary features cited in the "Diagnosis," above.

BIOLOGY AND FISHERIES.—Ribeiro and Petrere (1990) provided a summary of the life history and fishery for *Semaprochilodus taenurius* in the central portions of the Amazon basin. In that region, *S. taenurius* and *S. insignis*, both of which are identified under the common name of jaraquis, jointly "domi-

TABLE 22.—Morphometrics and meristics of *Semaprochilodus taeniurus:* (A) holotype of *Curimatus taeniurus*, MNHN A.8641 (specimen eviscerated, defleshed, dried and stuffed with straw), and (B) all specimens of *Semaprochilodus taeniurus* from which counts and measurements were taken (morphometric data for holotype of *Curimatus taeniurus* excluded from ranges as a consequence of method of preservation of specimen; see "Remarks"). Standard length is presented in mm; values 2 to 16 are percentages of SL, 17 to 21 are percentages of HL. Dash indicates datum unobtainable as a consequence of mode of preservation of holotype of *Curimatus taeniurus*, and question mark indicates specimen damaged for indicated feature.

Characters	A	B
	Morphometrics	
1. Standard length	162.1	25.2–281.1
2. Greatest body depth	27.8	31.5–41.3
3. Predorsal length	39.2	41.8–50.4
4. Dorsal-fin base length	16.2	15.6–21.2
5. Dorsal fin to adipose fin distance	31.5	20.2–32.3
6. Dorsal fin to caudal fin distance	48.9	35.7–50.4
7. Prepelvic length	46.6	47.0–62.5
8. Preanal distance	74.1	73.1–82.1
9. Snout to anal-fin insertion	77.1	75.6–88.5
10. Anal-fin base length	9.0	8.2–11.5
11. Caudal-peduncle length	15.7	11.5–15.2
12. Dorsal-fin length	17.0?	28.2–42.1
13. Pectoral-fin length	2.9?	14.6–22.8
14. Pelvic-fin length	8.6?	15.2–23.0
15. Least caudal-peduncle height	8.9	9.4–11.1
16. Head length	25.0	25.5–39.1
17. Snout length	32.8	30.0–38.5
18. Bony orbital diameter	28.8	25.0–33.3
19. Postorbital length	38.2	35.4–44.4
20. Interorbital width	43.8	41.7–53.3
21. Mouth width	32.8	30.3–45.5
	Meristics	
Lateral-line scales	74	64–77
Scale rows between dorsal-fin origin and lateral line	13	12–14
Scale rows between anal-fin origin and lateral line	9	9–11
Scale rows between pelvic-fin insertion and lateral line	14	12–14
Rows of scales around caudal peduncle	22?	23–26
Median predorsal scales	20	14–22
Median scales between dorsal and adipose fins	24	19–26
Vertebrae	–	42–43
Inner row teeth, upper jaw	–	7–13
Inner row teeth, lower jaw	–	6–10

nate 90 per cent of the commercial fisheries" (Ribeiro and Petrere, 1990:208).

REMARKS.—The original description of *Curimatus taeniurus* (=*Semaprochilodus taeniurus* herein) by Valenciennes (1817:116) was based upon a specimen collected by Humboldt and Bonpland in the upper Rio Negro system of Brazil (see Papavero, 1971:38, map 1, for itinerary of that collecting expedition). The holotype (MNHN A.8641) is a dry, presumably mostly defleshed, specimen stuffed with straw and is, furthermore, in poor condition probably as a consequence of its age. Nonetheless, the high lateral-line scale count (74) present in the holotype of *Curimatus taeniurus* only occurs in what is herein considered to be *S. taeniurus* within the family Prochilodontidae. Furthermore, Valenciennes (1817:166; 1850:86) mentioned the presence in *Curimatus taeniurus* of three longitudinal dark stripes on each caudal-fin lobe and a dark band across the middle rays of the caudal fin at the level of the lateral line. These meristic and pigmentary features, in combination, make it clear that Valenciennes' *Curimatus taeniurus* is conspecific with the samples that are herein considered to be *Semaprochilodus taeniurus*. Perhaps as a consequence of its distinctive high number of lateral-line scales and relatively elongate body, there have been relatively few misidentifications of this species in the literature subsequent to its original description.

MATERIAL EXAMINED.—190 specimens (31, 25.2–281.1 mm SL).

BRAZIL. *Amazonas:* Rio Maicurú, vicinity of Monte Alegre, NRM 19553, 1. Manaus (3°06'S, 60°00'W), BMNH 1913.7.7:4, 1 (1, 181.0); BMNH 1913.7.25:3, 1 (1, 55.2); MCZ 20134, 2 (223.0–245.0); MZUSP 9578, 1 (198.6); MZUSP 19293, 1 (138.5); NRM 19529, 1; USNM 167826, 1 (1, 179.0); USNM 290145, 1 (1, 208.4) [1R]; USNM 290147, 3 (3, 72.0–84.2). Manaus, Rio Amazonas (3°06'S, 60°00'W), CAS 59322, 3 (1, 197.7–203.1) [3R]; CAS-SU 39296, 3 (2, 134.8–152.3) [3R]. Rio Negro, Manaus (3°06'S, 60°00'W), CAS 6381, 1 (1, 169.8); MZUSP 6680, 7 (132.6–158.0). Igarapé Mauá, Manaus (3°06'S, 60°00'W), MZUSP 4623–4625, 3 (141.6–158.4). Lago do Aleixo, Rio Negro, CAS-SU 39294, 1 (1, 216.1); MCZ 20099, 1 (140.0); MCZ 20100, 1 (230.0). Ilha da Marchantaria (3°10'S, 59°45'W), USNM 289798, 2 (2, 114.0–125.7); USNM 290072, 1 (1, 65.2); USNM 290122, 1 (1, 40.4). "Ressaca" on Ilha da Marchantaria (3°10'S, 59°45'W), USNM 290070, 1 (1, 133.6) [1R]. Camaleão, Ilha da Marchantaria (3°10'S, 59°45'W), USNM 290068, 1 (1, 30.7). Ilha da Marchantaria, near Manaus (3°10'S, 59°45'W), USNM 229149, 2 (2, 71.6–77.0) [2R]. Reserva Ecológica de Anavilhanas, Rio Negro, Município de Novo Airão, MZUSP 27362, 1 (202.6). Rio Negro, between Manaus and Moura, MCZ 20158, 5 (210.0–235.0). Mouth of Rio Paduaú, Rio Negro, Airão Velho, MZUSP 27363, 5 (138.4–161.6). Pedra do Gavião, Rio Negro, Município de Moura, MZUSP 27365, 3 (144.1–152.1). l'Amerique Equioxiale (=Equatorial America), probably Brazil, Amazonas, upper Rio Negro, MNHN A.8641, 1 (162.1, holotype of *Curimatus taeniurus*). Rio Solimões, in Tefé and vicinity (approximately 3°24'S, 64°45'W), CAS-SU 39297 (formerly MCZ 20252), 1 (114.6); MCZ 20051, 1 (1, 227.2); MCZ 20102, 3 (157.0–167.0). Mouth of Rio Japurá, Rio Solimões, Tefé (3°24'S, 64°45'W), MZUSP 27392, 1 (123.3). Paraná do Lago Aruanã, below Japurá, Tefé (3°24'S, 64°45'W), MZUSP 27364, 4 (86.5–112.3). Manacapuru, Rio Solimões (3°06'S, 61°30'W), BMNH 1925.10.28:64–72, 9 (1, 142.0–161.3); NRM 17148, 1; USNM 162816, 1 (150.3; formerly BMNH 1925.10.28:73, in part). Lago Grande de Manacapuru, Manacapuru (3°06'S, 61°30'W), MCZ 20115, 8 (134.0–154.0). Rio Jutaí, tributary to Rio Solimões (approximately 2°31'S, 67°22'W), MCZ 20148, 13 (107.0–124.0); MCZ 20149, 2 (231.0–255.0). Rio Içapó, mouth of Rio Jutaí (approximately 2°31'S, 67°22'W), MZUSP 21024, 1 (262.7). Paraná do Janauacá, entrance to Lago

Castanho (3°28′S, 60°17′W), USNM 290069, 2 (2, 25.1–25.2). Lago Janauacá, Rio Solimões (3°28′S, 60°17′W), MZUSP 21562, 4 (178.1–217.2). Paraná do Janauari, MCZ 20155, 2 (210.0–230.0); MCZ 20156, 2 (166.0–166.1). Tonantins, Rio Amazonas (2°47′S, 67°47′W), MNHN 09.247–252, 6 (1, 115.3–158.2). Rio Tonantins, in Tonantins (2°47′S, 67°47′W), MCZ 20068, 8 (96.0–130.0). Tabatinga, MCZ 20086, 1 (112.0). Fonte Boa, Rio Solimões (2°03′S, 66°01′W), MCZ 20105, 6 (121.0–162.0). Parintins and vicinity (approximately 2°36′S, 56°44′W), MCZ 20127, 4 (159.0–228.0). Lago Coari, Rio Solimões, Coari (4°05′S, 63°08′W), MCZ 20062, 4 (205.0–236.0). Lago Saracá, in Silves, MCZ 20096, 5 (200.0–224.0). Rio Içá, tributary to Rio Solimões, border between Brazil and Colombia (3°07′S, 67°58′W), MCZ 20112, 6 (135.0–235.0). Rio Maués, Maués, Rio Madeira, MCZ 20074, 3 (145.0–206.0). Jatuarana, Rio Roosevelt, MCZ 20088, 1 (244). Lago Supiá, in front of Codajás, MZUSP 9674, 1 (205.2). Itacoatiara, Rio Amazonas, MZUSP 13489–13492, 4 (1, 204.3–230.8). Lago Beruri, Rio Purus (3°52′S, 61°20′W), MZUSP 6378, 2 (157.9–169.8). *Pará:* Santarém (2°26′S, 54°42′W), MCZ 20078, 4 (203.0–240.0); MNHN 09.63, 1 (1, 224.7). Riacho Urara, tributary of Rio Amazonas CAS 58891, 1 (1, 92.3) [1R]. Rio Tapajós, Santarém (2°26′S, 54°42′W), CAS-SU 58884, 2 (2, 111.0–123.0) [2R]. Ilha Japaiuna, Rio Tapajós, MZUSP 21349, 1 (170.5). Porto de Mós, MCZ 20109, 1 (120.0). Óbidos (1°52′S, 55°30′W), MCZ 20139, 8 (139.0–115.0). Rio Tapajós, MCZ 20163, 2 (194.0–198.0). Rio Trombetas, Oriximiná (1°45′S, 55°32′W), MZUSP 5457, 1 (215.5). Lago Grande, Rio Amazonas, CAS 59321, 1 (1, 131.1). *Rondônia:* Paraíso, Rio Machado (approximately 3°45′S, 59°03′W), MZUSP 14043, 1 (218.3). *Roraima:* Rio Branco, beach at Paraná Marará, MZUSP 29255, 1 (1, 270.6) [1R]; MZUSP 29261, 1 (1, 281.1) [1R]. *Inexact Locality:* Rio Amazonas, USNM 52545, 2 (1, 237.7); USNM 290375, 1 (220.0).

Semaprochilodus varii Castro, 1988

FIGURES 69, 71; TABLE 23

Prochilodus insignis [not of Jardine, 1841].—Pellegrin, 1909b:155 [in part, French Guiana].—Eigenmann, 1910:424 [in listing of South American fishes; in part, citations from the Guianas].

Semaprochilodus insignis [not of Jardine, 1841].—Mago-Leccia, 1972:60 [in part, report of occurrence of species in Guianas].—Géry, 1977:215 [in part, citation of presence of species in Guianas].—Géry and Planquette, 1983:70 [French Guiana, Saut Setatétéi].—Le Bail et al., 1984:58 [French Guiana].

Semaprochilodus varii Castro, 1988:503 [type locality: Suriname, Marowijne District, Marowijne River, about 25 km south of Albina].—Vari and Howe, 1991:39 [paratype depository].—Oyakawa, 1996:496 [paratype depository].—Planquette et al., 1996:137, fig. [French Guiana, Fleuve Maroni].

DIAGNOSIS.—*Semaprochilodus varii* is distinguished from *S. insignis, S. kneri,* and *S. taeniurus* by its possession of intense dark pigmentation on the membranous posterior portion of the operculum and on the exposed portion of the pectoral girdle that is absent in those three species. *Semaprochilodus varii* is, in turn, readily separated from *S. brama* and *S. laticeps,* which also lack such dark pigmentation, by the number of scales along the lateral line (39 to 41 versus 56 to 68, and 48 to 56, respectively), the number of horizontal rows of scales between the dorsal-fin origin and the lateral line (8 versus 11 to 13, and 10 or 11, respectively), and the number of horizontal rows of scales around the caudal peduncle (16 versus 23 to 27, and 19 to 24, respectively).

DESCRIPTION.—Morphometric and meristic data for *Semaprochilodus varii* presented in Table 23. Body high and transversely compressed. Greatest body depth at dorsal-fin origin. Dorsal profile of head slightly concave. Predorsal profile of body convex. Dorsal profile of body distinctly posteroventrally inclined along dorsal-fin base; profile straight from posterior of dorsal-fin base to adipose-fin origin and concave along caudal peduncle. Predorsal portion of body with obtuse median ridge. Postdorsal portion of body obtusely rounded transversely. Ventral profile of body distinctly convex from tip of lower jaw to posterior of anal-fin base. Ventral profile of caudal peduncle concave. Prepelvic region of body somewhat transversely flattened anteriorly, distinctly flattened proximate to pelvic-fin insertion. Pronounced ventral keel present between pelvic-fin insertion and anus.

Head profile obtusely pointed. Mouth slightly subterminal. Snout length slightly greater than, or equal to, horizontal width of orbit. Nares of each side of head close to each other; anterior nares circular, posterior nares crescent shaped. Adipose eyelid present but poorly developed; most developed along anterior portion, but with greater part of eye uncovered. Lips fleshy, less developed than in *Ichthyoelephas* and *Prochilodus,* and forming oral disk when protracted.

Functional teeth in two rows in each jaw. All teeth movably implanted in flesh that overlies jaws. All teeth of similar size, with exposed portions spoon shaped except when worn down. Inner tooth series in each jaw with 10 to 15 teeth on left side of upper jaw and 7 to 9 teeth on left side of lower jaw. Outer row of teeth in each jaw with approximately 80 teeth on each side of upper jaw and approximately 65 teeth on each side of lower jaw in holotype.

Scales cycloid. Scales in middorsal series between posterior of dorsal-fin base and adipose-fin origin similar in form to those of adjoining regions of body, but with membranous spatulate process along posterior border of each scale in that series. Lateral line with 39 to 41 (75.0% of specimens with 41) pored scales; 8 horizontal rows of scales between dorsal-fin origin and lateral line; 8 horizontal rows of scales between pelvic-fin insertion and lateral line; 6 or 7 (75.0% of specimens with 6) horizontal rows of scales between anal-fin origin and lateral line; 10 to 13 (41.7% of specimens with 11 or 12) median predorsal scales; 11 to 15 (45.8% of specimens with 12) scales in middorsal series between posterior of dorsal-fin base and adipose-fin origin; 16 horizontal rows of scales around caudal peduncle.

TABLE 23.—Morphometrics and meristics of *Semaprochilodus varii:* (A) holotype of *Semaprochilodus varii,* ZMA 106.222; (B) paratypes of *Semaprochilodus varii,* AMNH 16406, MZUSP 37177–78, USNM 285719, ZMA 106.372, and ZMA 119.877; and (C) all specimens of *Semaprochilodus varii* from which counts and measurements were taken. Standard length is presented in mm; values 2 to 16 are percentages of SL, 17 to 21 are percentages of HL.

Characters	A	B	C
		Morphometrics	
1. Standard length	66.3	55.5–279.6	55.5–279.6
2. Greatest body depth	47.5	43.5–48.3	41.2–48.3
3. Predorsal length	49.8	47.2–51.0	45.0–51.3
4. Dorsal-fin base length	19.5	17.6–21.4	16.8–21.4
5. Dorsal fin to adipose fin distance	24.1	21.0–26.0	21.0–26.7
6. Dorsal fin to caudal fin distance	40.1	37.8–42.1	37.8–42.1
7. Prepelvic length	54.8	51.3–57.6	51.2–57.6
8. Preanal distance	77.8	77.7–83.4	77.4–83.4
9. Snout to anal-fin insertion	81.7	81.2–85.6	81.1–85.6
10. Anal-fin base length	13.0	11.6–13.6	10.6–13.6
11. Caudal-peduncle length	11.9	11.5–14.4	11.4–14.4
12. Dorsal-fin length	34.4	29.1–43.6	29.0–43.6
13. Pectoral-fin length	20.7	20.3–22.9	20.3–23.1
14. Pelvic-fin length	22.2	15.3–24.4	15.3–24.4
15. Least caudal-peduncle height	12.0	11.2–12.7	11.2–12.9
16. Head length	31.7	29.4–33.7	29.2–33.7
17. Snout length	39.0	32.5–41.2	32.5–43.0
18. Bony orbital diameter	30.0	22.9–33.5	22.9–36.2
19. Postorbital length	34.3	34.0–39.0	34.0–39.0
20. Interorbital width	45.2	43.5–48.1	43.4–53.2
21. Mouth width	41.9	40.9–46.2	38.5–46.2
		Meristics	
Lateral-line scales	41	40–41	39–41
Scale rows between dorsal-fin origin and lateral line	8	8	8
Scale rows between anal-fin origin and lateral line	6	6–7	6–7
Scale rows between pelvic-fin insertion and lateral line	8	8	8
Rows of scales around caudal peduncle	16	16	16
Median predorsal scales	10	10–12	10–13
Median scales between dorsal and adipose fins	12	11–13	11–15
Vertebrae	37	36–37	36–37
Inner row teeth, upper jaw	15	11–15	10–15
Inner row teeth, lower jaw	9	7–9	7–9

Dorsal fin preceded by small, but well-developed, anteroventrally bifurcate, procumbent spine somewhat triangular in lateral view. Dorsal-fin rays (including procumbent spine) iii,10 [iii,10]; anal-fin rays iii,8 [iii,8]; pectoral-fin rays i,14 to 17 (i,15 most frequent) [i,15]; pelvic-fin rays i,7 or 8 (i,8 most frequent) [i,8]; principal caudal-fin rays 10/9 [10/9].

Vertebrae 36 or 37 (84.2% of specimens with 37).

Dorsal fin distally elongate; posterior unbranched and anterior branched rays longest and subequal. Dorsal-fin origin located closer to tip of snout than to caudal-fin base. Greatest length of adipose fin approximately two-thirds of horizontal width of eye. Adipose-fin origin located along vertical that passes through middle of anal-fin base. Pectoral fin pointed distally. Tip of adpressed pectoral fin reaching posteriorly to, or almost to, pelvic-fin insertion. Pelvic fin falcate. Pelvic-fin insertion located slightly posterior to vertical that passes through dorsal-fin origin. Tip of adpressed pelvic fin reaching posteriorly approximately two-thirds of distance between pelvic-fin insertion and anus. Axillary scale present, its length approximately one-third of greatest length of pelvic fin. Posterior unbranched and anterior branched anal-fin rays longest and subequal. Caudal fin moderately bifurcate.

COLORATION IN ALCOHOL.—Ground coloration silvery yellow, with dorsal portions of body and head darker. Lateral surface of body with approximately 13 dark, wavy, horizontal stripes along dorsal and ventral margins of exposed portions of scales (stripes not apparent in large specimens examined (e.g., NRM 28388) that retain large amounts of guanine on scales (see also Figure 71), but see Castro (1988, fig. 1) for illustration of specimens in which body stripes apparent). Approximately 7 wavy stripes dorsal to, and 6 wavy stripes ventral to, lateral line. When guanine missing, probably as consequence of acidity of original fixative, stripes somewhat irregular on caudal peduncle. Dense field of brown or black chromatophores forming distinct dark region on membranous portion of opercle and on lateral exposed portion of pectoral girdle.

Dorsal fin with 3 to 5 irregular dark stripes beginning on anterior margin of fin and extending across fin approximately parallel to base of fin. Adipose fin with dusky border. Pectoral and pelvic fins dusky. Base coloration of anal fin hyaline, with fields of dark chromatophores forming 1 to 5 [5] irregular oblique stripes extending across fin, with anterior stripes running parallel to each other. Caudal fin with 7 to 14 dark stripes; one horizontal stripe overlying middle caudal-fin rays, 3 to 6 oblique stripes on upper lobe, and 3 to 7 stripes on lower lobe, of caudal fin. Iris silvery yellow, with diffuse dusky areas on dorsal and ventral portions.

COLORATION IN LIFE (Based upon a photograph in Planquette et al. (1996:137) of an apparently recently collected specimen).—Overall coloration bright silver, darker on dorsal portions of head and body. Dark pigmentation as described above. Caudal fin somewhat yellowish. Distal portion of lower lobe of dorsal fin and distal portion of anterior region of anal fin reddish (latter fin damaged in photographed specimen). Dorsal and ventral portions of iris golden brown.

DISTRIBUTION.—*Semaprochilodus varii* is endemic to the Marowijne River-Fleuve Maroni system of Suriname and French Guiana, respectively (Figure 69, dots). Planquette et al. (1996:137) indicated that *S. varii* is widespread throughout that river basin.

COMMON NAME.—Colmata, Couliata, Courimata, Koulimata. Koumata, Péni-Kwimata (French Guiana=Guyane).

REMARKS.—Castro's (1988:503–508, figs. 1, 2) description of *Semaprochilodus varii* was based upon material collected in the Marowijne River, Suriname (the Fleuve Maroni of French Guiana). The extensive collecting efforts throughout French Guiana reported on by Planquette et al. (1996) demonstrated the species to be broadly distributed through, and apparently

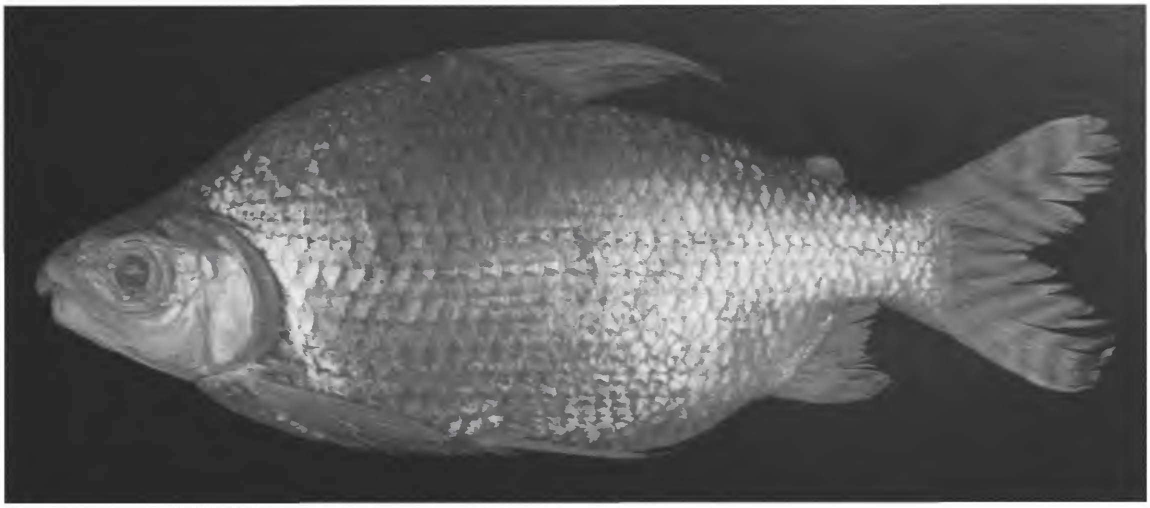


FIGURE 71.—*Semaprochilodus varii*, NMW 56649, 246.5 mm SL; Suriname, Marowijne, Albina.

endemic to, that river system (Planquette et al., 1996:137). Examination of the specimen collected by Mélinon in French Guiana and reported on by Pellegrin (1909b:154–155) as *Prochilodus insignis* revealed that it is *Semaprochilodus varii*, which is the only member of the genus that is known to occur in the Guianas.

Citations of *Semaprochilodus insignis* from the Marowijne-Maroni basin by Géry (1977:215), Géry and Planquette (1983: 70), and Le Bail et al. (1984:58) are apparently erroneous because no specimens of that species that originated in that river system were examined during the course of this study. These reports are all consequently considered to be based upon specimens of *S. varii*, the only member of the genus known to occur in that drainage basin. The citation of *S. insignis* for the Guianas by Mago-Leccia (1972:60) was, apparently, not based upon specimens examined by that author but rather was probably derived from an earlier report of that species from the region, perhaps that of Pellegrin (1909b:155) for French Guiana, and as such it is considered herein to refer to *S. varii*.

MATERIAL EXAMINED.—25 specimens (24, 55.5–279.6 mm SL).

FRENCH GUYANA. *Saint Laurent du Maroni:* Fleuve Maroni, MNHN 95-85-86, 2 (2, 77.0–80.5). Maripasoula, small tributaries to Fleuve Maroni, approximately 2 hours upstream from Maripousola (3°30′33″N, 54°00′28″W), NRM 28388, 1 (258.8). *Inexact Locality:* French Guiana, MNHN A.9778, 1 (1, 279.0).

SURINAME. *Marowijne:* Albina, NMW 56649, 56650, 2 (2, 246.5–257.2) [1R]. Marowijne River, approximately 25 km S of Albina, MZUSP 37177–78, 2 (2, 65.1–69.9, paratypes of *Semaprochilodus varii*) [2R]; USNM 285719, 4 (4, 59.6–64.7, paratypes of *Semaprochilodus varii*) [3R]; ZMA 106.222, 1 (1, 66.3, holotype of *Semaprochilodus varii*) [1R]; ZMA 106.372, 5 (5, 60.5–73.4, paratypes of *Semaprochilodus varii*) [5R]; ZMA 119.877, 6 (6, 55.5–72.4, paratypes of *Semaprochilodus varii*) [6R]. Litani and Oelemari Rivers, AMNH 16406, 1 (1, 279.6, paratype of *Semaprochilodus varii*) [1R].

Phylogenetic Biogeography of the Prochilodontidae

The limited resolution of the interspecific phylogenies for *Prochilodus* and *Semaprochilodus* limits the possible statements concerning the historical biogeography of the Prochilodontidae. Nonetheless, the available information is informative as to several aspects of the history of the family.

Prochilodus occurs to both sides of the Andean Cordilleras (Figures 30, 43, 52), and it is the only genus in the Prochilodontidae with such a distribution. *Prochilodus magdalenae* inhabits the rivers to the west of the northern potions of the main Cordilleras of the Andes, including the Sierra de Perija, with *P. reticulatus*, in turn, endemic to the rivers of the Lago Maracaibo basin between the Sierra de Perija to the west and the Cordillera da Merida in the east. The 11 remaining species of *Prochilodus* occur east of the Andean Cordilleras from the Río Orinoco basin south to the Río de la Plata system. *Ichthyoelephas* and *Semaprochilodus*, sister genera according to the phylogeny arrived at in this study, also have a relationship across the Andes. *Ichthyoelephas* has a totally Trans-Andean distribution in the rivers of northwestern Colombia and western Ecuador, whereas *Semaprochilodus* only occurs east of the Andean Cordilleras in the Río Orinoco, Rio Amazonas, and Fleuve Maroni-Morawijne River systems along the Suriname-French Guiana border region.

These distributions and the fact that prochilodontids are inhabitants of lowland drainages and low-elevation upland rivers indicate that the family Prochilodontidae, at least the basal components of *Prochilodus*, and the ancestor of the clade formed by *Ichthyoelephas* and *Semaprochilodus* had evolved prior to the final uplift of the Andes that completely separated the lowlands faunas to each side of the mountain chain. As noted under "Bauplan shifts and Evolutionary Stasis," above, the last closure of the Maracaibo-Falcon outlet of the Río Orinoco through what is now a portion of Trans-Andean South America, occurred about eight million years ago during the final uplift of the northern portions of the Andean Cordilleras (Lundberg et al., 1998:9, fig. 20). *Prochilodus magdalenae*, however, is distributed through several river systems to the west of the main Cordilleras of the Andes, the portion of the Andean mountain chain that includes the Sierra de Perija. The Sierra de Perija arose approximately 11.8 million years ago, as indicated by the westward shift of paleocurrents in the Río Magdalena valley (Lundberg et al., 1998:37). This uplift of the Sierra de Perija would represent the minimal age for *Prochilodus*. Because of the occurrence of at least one *Ichthyoelephas* species in those same western drainage basins, and given that *Ichthyoelephas* is the sister group to *Semaprochilodus* that has an entirely Cis-Andean distribution, we hypothesize that the ancestor of the clade formed by *Ichthyoelephas* and *Semaprochilodus* similarly was present to the two sides of what are now the western Cordilleras of the northern Andes at some point prior to this final uplift of the Colombian-Venezuelan Eastern Cordillera of the Andes approximately 11.8 millions years ago.

A comparable pattern of relationships across the Andean Cordilleras has been found in other groups of Neotropical freshwater fishes, including three genera of the Curimatidae, the sister group to the Prochilodontidae (*Cyphocharax*, Vari, 1992; *Potamorhina*, Vari, 1984; *Steindachnerina*, Vari, 1991), which are distributed across the phylogeny of the Curimatidae (Vari, 1989a, fig. 44). Given the sister-group relationship between the Prochilodontidae and the Curimatidae (Vari, 1983, 1989a), the divergence between the common ancestor of those two families obviously significantly predates the 11.8 million year estimate assuming a steady rate of cladogenesis. Although we know of no literature citations of fossils identifiable as prochilodontids, Malabarba (1997) demonstrated that a fossil curimatid species originally described by Travassos and Santos (1955) from the Taubaté formation of São Paulo, Brazil, as *Curimata mosesi* was assignable to the curimatid genus *Cyphocharax*, a component of a relatively derived assemblage within the Curimatidae. Reis (1998:360), in his analysis of the fossil record of various groups of Neotropical freshwater fishes, noted that the assignment of *Curimata mosesi* to *Cyphocharax* within the context of the phylogeny for the Curimatidae and closely related families (Curimatidae, Prochilodontidae, Anostomidae, Chilodontidae) proposed by Vari (1983, 1989a), and further supported by new evidence in this study, provided minimal ages for a number of clades not only within the Curimatidae but for each of these families. The sediments in which *Cyphocharax mosesi* was found were at least 22.5 million years old (Oligocene); therefore, not only was *Cyphocharax* extant by that time period, but so were the majority of other genera in the Curimatidae. Because the Prochilodontidae is the sister group to the Curimatidae, it must be at least as old as the Curimatidae. The similar situation applies to the Chilodontidae and Anostomidae that are, in turn, the sister taxa to the clade that consists of the Curimatidae plus Prochilodontidae (Reis, 1998, fig. 18). Thus, the hypothesis of evolutionary stasis for *Prochilodus* for 11.8 million years and the hypothesis that the Prochilodontidae and the ancestor of the clade formed by *Ichthyoelephas* and *Semaprochilodus* were extant at least by that period is congruent with present-day distributional evidence and with information available from the fossil record.

The lack of resolution at lower levels within the phylogeny of the Prochilodontidae makes it impossible to propose definitive statements about the historical biogeography of most prochilodontids with the exception of *Ichthyoelephas* and a component of *Semaprochilodus*. *Ichthyoelephas* includes two species with widely separated distributions to the west of the Andean Cordilleras: *I. longirostris* of the Caribbean Sea versant drainages of northwestern Colombia, and *I. humeralis*, which occurs in various Pacific Ocean slope rivers of western Ecuador. Interspecific disjunctions between Colombian and Ecuadorian drainages, albeit not as pronounced as that in *Ichthyoelephas*, occur in other groups (e.g., the genus *Pseudocurimata*, family Curimatidae, Vari, 1989a, fig. 18), but the complex geomorphological history and topography of the region makes it difficult to correlate such disjunctions with particular events in earth history. One potential vicariance event was the accretion of the Choco Block, which includes the main valleys of the Río San Juan and Río Atrato, to the northwestern corner of South America during and after the period of the middle Miocene (Lundberg et al., 1998:36).

In the case of *Semaprochilodus*, the phylogeny indicates that *S. kneri* of the Río Orinoco basin is the sister species to *S. insignis*, an endemic of the Rio Amazonas system. Sister-group relationships between species in those two basins occur in a variety of groups of fishes and may be associated with the uplift of the Vaupes Arch, which extends between the Guyana Shield in the east and the area of the Serrania de la Macarena in the west. This uplift led to the near complete separation of the Orinoco and Amazon basins during the Late Miocene (11.8–10.0 million years ago; Lundberg et al., 1998:40). The lack of resolution of the relationships among the three species in the other clade within *Semaprochilodus* precludes any definite statements as to the sequence of vicariance events; however, *S. brama* occurs in the Rio Xingú and Rio Tocantins basins and *S. laticeps* is endemic to the Río Orinoco basin and, thus, may demonstrate a similar biogeographic pattern. Alternatively, one of the other of those species may be more closely related to *S. varii* of the Fleuve Maroni-Marowijne River system of Suriname and French Guiana.

Resumo

As relações inter e intra-familiares dos Prochilodontidae foram investigadas utilizando-se sistemas anatômicos esqueléticos e não esqueléticos. As sinapomorfias encontradas fornecem evidências adicionais de que o clado formado pelos Prochilodontidae e Curimatidae é grupo irmão do clado composto pelos Anostomidae e Chilodontidae; fornecem suporte adicional ao monofiletismo dos Prochilodontidae; provêem evidências para a hipótese de que *Ichthyoelephas, Prochilodus* e *Semaprochilodus* sejam, cada um deles, linhagens monofiléticas; e de que *Prochilodus* seja grupo irmão do clado formado por *Ichthyoelephas* e *Semaprochilodus;* além de resolver parcialmente as relações intragenéricas.

O gêneros de Prochilodontidae reconhecidos são: *Ichthyoelephas* Posada Arango (1909), *Prochilodus* Agassiz (in Spix & Agassiz, 1829) e *Semaprochilodus* Fowler (Fowler, 1941). *Pacu* Agassiz (in Spix & Agassiz, 1829) e *Chilomyzon* Fowler (1906) são sinônimos de *Prochilodus.*

Ichthyoelephas inclui duas espécies: *I. humeralis* (Günther, 1859) dos Rios Guayas e Santiago, Equador ocidental; e *I. longirostris* (Steindachner, 1879) dos Rios Cauca-Magdalena e Rancheria, Colômbia. *Ichthyoelephas pataló* Posada Arango (1909) e *I. longirostris neglectus* Dahl (1971) são sinônimos de *I. longirostris.*

Prochilodus consiste de 13 espécies: *P. argenteus* Agassiz (in Spix & Agassiz, 1829), do Rio São Francisco e também introduzido em outros corpos d'água no nordeste do Brasil; *P. brevis* Steindachner (1874), dos rios costeiros de porte pequeno a médio no nordeste do Brasil e também de dois pequenos afluentes da margem esquerda do baixo Rio São Francisco; *P. britskii* Castro (1993), do Rio Tapajós; *P. costatus* Valenciennes (in Cuvier & Valenciennes, 1850), do Rio São Francisco e também introduzido no Rio Jequitinhonha; *P. hartii* Steindachner (1874), dos Rios Pardo e Jequitinhonha, nos Estados de Minas Gerais e Bahia; *P. lacustris* (1907), dos Rios Mearim e Parnaíba, nordeste do Brasil; *P. lineatus* (Valenciennes, 1836), dos Rios Paraíba do Sul e Jacuí, no sudeste e sul do Brasil, respectivamente, e sistema do Paraná-Paraguai-La Plata, excluindo o Rio Iguaçu, em vários países; *P. magdalenae* Steindachner (1879), dos Rios Atrato, Sinú, Rancheria e Cauca-Magdalena, Colômbia; *P. mariae* Eigenmann (1922), do Rio Orinoco; *P. nigricans* Agassiz (in Spix & Agassiz, 1829), do Rio Tocantins e amplamente distribuído em toda bacia Amazônica, em vários países; *P. reticulatus* Valenciennes (1850), dos rios da bacia de drenagem do Lago Maracaibo, Venezuela; *P. rubrotaeniatus* Jardine (1841), dos Rios Branco e Marauiá, Brasil, Río Caroni, Venezuela, e também dos rios costeiros das Guianas; e *P. vimboides* Kner, 1859, dos rios costeiros do Brasil entre os Rios Jequitinhonha e Paraíba, porções orientais do alto Rio Paraná e porção superior do Rio São Francisco.

Prochilodus cearensis Steindachner (1911) é um sinônimo de *P. brevis. Prochilodus affinis* Lütken (1875) é um sinônimo de *P. costatus. Prochilodus scrofa* Steindachner (1881), *P. platensis* Holmberg (1888) e *Salmo novemradiatus* Larrañaga (1923) são sinônimos de *P. lineatus. Prochilodus beani* Eigenmann (in Eigenmann e Ogle, 1907) e *P. eigenmanni* Ahl (1937) são sinônimos de *P. magdalenae. Prochilodus ortonianus* Cope (1878), *P. cephalotes* Cope (1878), *P. caudifasciatus* Starks (1906), *Curimatus tigris* Fowler (1913), *Prochilodus beni* Pearson (1924) e *P. labeo* Loubens et al. (1991) são sinônimos de *P. nigricans. Prochilodus asper* Lütken (1875) é um sinônimo de *P. reticulatus. Prochilodus maripicru* Eigenmann (1912) é sinônimo de *P. rubrotaeniatus. Prochilodus oligolepis* Günther (1864) e *P. steindachneri* Fowler (1906) são sinônimos de *P. vimboides.*

Semaprochilodus contem seis espécies: *S. brama* (Valenciennes in Cuvier & Valenciennes, 1850), dos Rios Xingu e Tocantins; *S. insignis* (Jardine, 1841), da calha principal do Rio Amazonas e seus tributários; *S. kneri* (Pellegrin, 1909), do Rio Orinoco; *S. laticeps* (Steindachner, 1879), também do Rio Orinoco; *S. taeniurus* (Valenciennes in Humboldt &

Bonpland, 1817), da calha principal e afluentes do Rio Amazonas; e *S. varii* Castro (1988), do Rio Marowijne-Maroni, Suriname e Guiana Francesa. *Semaprochilodus squamilentus* Fowler (1941) é sinônimo de *S. brama. Prochilodus theraponura* Fowler (1906) e *P. amazonensis* Fowler (1906) são sinônimos de *Semaprochilodus insignis.*

Neótipos são designados para *Prochilodus argenteus* Agassiz e *P. nigricans* Agassiz. Lectótipos são designados para *Prochilodus affinis* Lütken, *P. asper* Lütken, *P. brevis* Steindachner, *P. cearensis* Steindachner, *P. hartii* Steindachner, *P. humeralis* Günther, *P. kneri* Pellegrin, *P. lacustris* Steindachner, *P. longirostris* Steindachner, *P. asper* var. *magdalenae* Steindachner, *P. oligolepis* Günther, *P. reticulatus* Valenciennes, *P. scrofa* Steindachner e *P. vimboides* Kner.

A análise da biogeografia filogenética dos Prochilodontidae indica que tanto a família como seus eventos cladogenéticos internos maiores possuem uma idade mínima de aproximadamente 12 milhões de anos. Apesar de grandes mudanças na morfologia geral caracterizarem a família Prochilodontidae e seus clados componentes maiores, a diversidade morfológica interna dos gêneros é relativamente pequena. Aparentemente, a morfologia geral do gênero *Prochilodus* tem permanecido estática por pelo menos 12 milhões de anos. Levando-se em conta o fato de Prochilodontidae e Curimatidae serem grupos irmãos (Vari, 1983, 1989a), a divergência a partir do ancestral comum de ambas as famílias obviamente antecede em muito os 12 milhões de anos estimados para *Prochilodus,* especialmente se uma taxa cladogenética constante for assumida.

Apesar não haver quaisquer citações na literatura científica de fósseis de Prochilodontidae, Malabarba (1997) demonstrou que *Curimata mosesi,* espécie fóssil descrita por Travassos & Santos (1955) da formação Taubaté, em São Paulo, Brasil, pertence ao genero *Cyphocharax,* componente de um subgrupo relativamente derivado de Curimatidae. Uma vez que os sedimentos onde *Curimata* (=*Cyphocharax*) *mosesi* foi encontrada possuem, no minimo, 22,5 milhões de anos de idade (Oligoceno), a idade mínima não só de *Cyphocharax* e também da maioria do outros generos de Curimatidae, assim como aquela de Prochilodontidae, e também a do clado Chilodontidae-Anostomidae, clado irmão de Curimatidae-Prochilodontidae, deve ser 22,5 milhões de anos. Assim, nossa hipótese de estase evolutiva de aproximadamente 12 milhões de anos para *Prochilodus,* além daquela estimando um idade mínima equivalente tanto para a família Prochilodontidae como um todo, quanto para o ancestral comum do clado formado por *Ichthyoelephas* e *Semaprochilodus,* é inequivocamente conservadora a luz das informações provenientes do registro fóssil.

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Index of Generic and Species Synonymies and Species Accounts

(Pages of principle discussions of genera and species in italics)

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