

Phylogenetic Relationships  
of the Families Curimatidae,  
Prochilodontidae, Anostomidae,  
and Chilodontidae  
(Pisces: Characiformes)

RICHARD P. VARI

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Phylogenetic Relationships of the  
Families Curimatidae, Prochilodontidae,  
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*Richard P. Vari*



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## ABSTRACT

Vari, Richard P. Phylogenetic Relationships of the Families Curimatidae, Prochilodontidae, Anostomidae, and Chilodontidae (Pisces: Characiformes). *Smithsonian Contributions to Zoology*, number 378, 60 pages, 41 figures, 1 table, 1983.—A series of osteological and soft anatomical systems in the families Curimatidae, Prochilodontidae, Anostomidae, and Chilodontidae were examined to reconstruct the phylogenetic relationships of these taxa and determine whether they are a monophyletic assemblage. Numerous adaptations associated with the food gathering and manipulation systems along with those in other portions of the body provided data useful in the reconstruction of the phylogenetic relationships of these taxa. The evidence of this study is congruent with the hypothesis that the four families constitute a monophyletic assemblage definable by shared derived characters. Results of the analysis indicate that the Curimatidae and Prochilodontidae are most parsimoniously interpreted to be sister groups. The assemblage formed by those two families is considered to be the sister group of the monophyletic lineage that consists of the Anostomidae and Chilodontidae. Synapomorphies define the members of each family as monophyletic units.

The well-developed epibranchial organs in the Chilodontidae, Citharinidae, and the Curimatidae plus Prochilodontidae, were found to represent three distinct, nonhomologous kinds of pharyngeal outpocketings. The most parsimonious interpretation of those data and other available information on ostariophysan phylogeny is that such diverticuli have been acquired several times independently among characiforms and their near relatives. This conclusion agrees with the hypothesis proposed by Nelson (1967) but indicates that Bertmar, Kapoor, and Miller's concept (1969) of epibranchial organs as the ancestral condition for teleosts is not parsimonious, at least when applied to ostariophysan fishes.

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# Phylogenetic Relationships of the Families Curimatidae, Prochilodontidae, Anostomidae, and Chilodontidae (Pisces: Characiformes)

*Richard P. Vari*

## Introduction

The Curimatidae, Prochilodontidae, Anostomidae, and Chilodontidae form a speciose, morphologically diverse assemblage of characiform fishes widely distributed in Neotropical freshwaters. Members of these families occur in the Atlantic drainages of South America from northern Colombia to the Río Negro of Argentina and inhabit the rivers and streams of the Pacific drainages of the region from Puntarenas Province of Costa Rica south to central Peru. Curimatids, prochilodontids, anostomids, and chilodontids inhabit a broad variety of freshwater ecosystems ranging from stagnant ox-bow lakes through sluggish rivers to rapidly flowing streams. In certain ecological settings they represent a significant proportion of the fish biomass (Lowe-McConnell, 1975:109), and many members of these taxa are exploited by commercial and subsistence fisheries throughout the Neotropics (Lowe-McConnell, 1975:74; Smith, 1981:140; Goulding, 1981:60).

The results reported in this paper are an outgrowth of phylogenetic and revisionary studies originally centered on the Curimatidae. An effec-

tive analysis of phylogenetic relationships within that family necessitated the recognition of an appropriate outgroup, thereby allowing the polarization of intrafamilial character variation. A prerequisite for the determination of the sister group to curimatids was an explicit, corroborated hypothesis of the phylogenetic placement of curimatids within a taxonomically more encompassing assemblage of characiforms.

Widely divergent opinions have been advanced on the exact relationships of the Curimatidae to other characiforms (Table 1). Günther (1864:288) united the then-known members of the Curimatidae (*Curimatus*), Prochilodontidae (*Prochilodus*), Chilodontidae (*Caenotropus*), Hemiodontidae (*Hemiodus*), and Parodontidae (*Saccodon*, *Parodon*) (families sensu Greenwood et al., 1966) in his suprageneric group Curimatina, and placed the described genera of the present day Anostomidae (*Anostomus*, *Rhytiodus*, *Leporinus*) in the Anostomatina group. Boulenger (1904:576), in a significant shift, incorporated the Neotropical curimatids (*Curimatus*) and prochilodontids (*Prochilodus*) into his subfamily Citharininae, together with the Old World characiform genera *Citharinus* and *Citharidium*. His Anostominae included the present day anostomids (*Anostomus*, *Leporinus*, *Nanognathus* [? = *Schizodon*]) and genera today considered

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TABLE 1.—Classifications of the four-family assemblage discussed in the text

Author	Classification
Günther, 1864	Curimatina group <i>Curimatus</i> , <i>Prochilodus</i> , <i>Caenotropus</i> , <i>Hemiodus</i> , <i>Saccodon</i> , <i>Parodon</i>
	Anostomatina group <i>Anostomus</i> , <i>Rhytiodus</i> , <i>Leporinus</i>
Boulenger, 1904	Characinae [in part] Citharinae <i>Citharinus</i> , <i>Citharidium</i> , <i>Curimatus</i> , <i>Prochilodus</i>
	Anostominae <i>Anostomus</i> , <i>Leporinus</i> , <i>Characidium</i> , <i>Chorimycteris</i> , <i>Nanostomus</i> , <i>Nanognathus</i>
	Hemiodontinae <i>Caenotropus</i> , <i>Hemiodus</i> , <i>Saccodon</i> , <i>Parodon</i>
Regan, 1911	Anostomidae Curimatinae <i>Curimatus</i> , <i>Anodus</i>
	Prochilodontinae <i>Prochilodus</i>
	Anostominae <i>Anostomus</i> , <i>Rhytiodus</i> , <i>Leporinus</i> , <i>Leporellus</i> , <i>Caenotropus</i>
Gregory and Conrad, 1938	Anostominae (=Anostomidae of Regan, 1911)
Greenwood et al., 1966	Curimatidae, Prochilodontidae, Anostomidae, Chilodontidae
Géry, 1977b	Anostomidae Anostominae <i>Schizodon</i> , <i>Leporinus</i> , <i>Abramites</i> , <i>Rhytiodus</i> , <i>Anostomoides</i> , <i>Anosto-</i> <i>mus</i> , <i>Synaptolaemus</i> , <i>Sartor</i> , <i>Gnathodolus</i>
	Leporellinae <i>Leporellus</i>
	Curimatidae Chilodinae <i>Caenotropus</i> , <i>Chilodus</i>
	Prochilodinae <i>Semaprochilodus</i> , <i>Prochilodus</i> , <i>Ichthyocephalus</i>
	Curimatinae <i>Curimata</i> , <i>Curimatella</i> , <i>Curima-</i> <i>topsis</i>
	Anodinae <i>Anodus</i>

either characids (*Characidium*, *Chorimycteris* [= *Characidium*]) or lebiasinids (*Nanostomus* [= *Nanostomus*]). The chilodontid taxa described at that time (*Caenotropus* with *Chilodus* as a synonym) were united by Boulenger in the Hemiodontidae together with various hemiodontids (*Hemiodus*) and parodontids (*Saccodon*, *Parodon*). Regan (1911:20) rejected Boulenger's transatlantic grouping of Neotropical curimatids and prochilodontids with some Old World characiforms. Furthermore, he disagreed with Günther's recognition of a separate taxon solely for anostomoids and that author's alignment of the chilodontids with hemiodontids. Rather, he incorporated the present day Curimatidae (*Curimatus*), Prochilodontidae (*Prochilodus*), Anostomidae (*Anostomus*, *Rhytiodus*, *Leporinus*, *Leporellus*) and Chilodontidae (*Caenotropus*) in his family Anostomidae with the last two groups combined in his subfamily Anostominae. Gregory and Conrad (1938:347) followed Regan in considering these four families to be a single taxon, but at the subfamily level. Eigenmann (1917:38-39), in contrast, placed the Anostominae, Chilodinae, Prochilodinae, Hemiodontinae, Elopomorphinae, and Curimatinae (= the Anostomidae, Chilodontidae, Prochilodontidae, Hemiodontidae, Anodinae, and Curimatidae of Greenwood et al., 1966) as "an offshoot of the Cheirodontinae" without any explicit comment on the relationships of the individual components.

Géry (1961:108) presented a dendrogram of his hypothesized phylogeny of anostomids and their presumed relatives. That outgroup included curimatids, prochilodontids, hemiodontids and lebiasinids but not chilodontids. However, exact concepts of phylogenetic relationship cannot be retrieved from Géry's figure (1961, fig. 24). More recently Géry (1977b:210) united curimatids, prochilodontids, chilodontids, and anodontines in his family Curimatidae but retained a separate Anostomidae for anostomids (see Table 1 for included genera). No explicit statement on the degree to which that classification reflects underlying phylogenetic concepts was provided, nor were the characters that support this grouping of taxa discussed.



The classifications summarized above generally were advanced without a discussion of the basis for the different groupings of taxa or with only a cursory presentation of the anatomical information underlying the taxonomic decisions of the different authors. The absence of such data made it impossible to determine the extent to which those classifications reflected phylogenetic rather than phenetic concepts. Thus, an evaluation of the relative merits of the classifications as phylogenetic indicators was difficult, if not impossible.

Roberts (1973:221) was the only author to explicitly state his concepts on the relationships of a subgroup of these four families and to detail the characters associated with his hypotheses. Contrary to his predecessors, Roberts rejected the hypothesis of a close phylogenetic relationship of the Curimatidae and Prochilodontidae. Rather he stated that "the evidence favoring relationship between Prochilodontidae and Anostomidae is relatively strong. . . ." He did not, however, comment on what relationship he envisioned for curimatids relative to the lineage purportedly formed by those two families or propose an alternative sister group for the Curimatidae.

Curimatids have, therefore, been inconsistently associated with a broad range of Neotropical and Old World characiform groups. Similarly, hypotheses on the relationships of prochilodontids, anostomids, and chilodontids to each other and characiform outgroups have differed in explicitness and inclusiveness. Furthermore, during the century-old discussion on the relationships of these families, no phylogenetic hypothesis has been put forward that uses criteria considered acceptable in this study: the possession of shared derived characters. The conjunction of these factors made it impossible to evaluate which, if any, of the previous classifications was an accurate representation of the phylogenetic history of curimatids and their close relatives. It was in an attempt to resolve this question that this study was undertaken.

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### Systematic Procedures

The relationships of the Curimatidae, Prochilodontidae, Anostomidae, and Chilodontidae are analyzed using the methodology of phylogenetic reconstruction first formalized by Hennig (1950, 1966). The goal of phylogenetic systematics (alternatively termed cladistics or cladism) is the grouping of taxa in a series of nested units that reflect the best estimate of the natural hierarchical history of groups of organisms.

Taxa are grouped on the basis of the possession of shared derived characters (synapomorphies), which are considered the only valid basis for hypotheses of common ancestry. Hypotheses of relationship derived from the possession of shared primitive characters (symplesiomorphies) and phylogenetic speculations based on concepts of overall phenetic similarity or degrees of difference are either not useful tests of phylogenetic hypotheses or incongruent with the aim of this study, that is, the advancement of hypotheses of the phylogenetic histories of the taxa under examination.

In keeping with the general scientific principle of parsimony, the hypothesis of the phylogenetic history of a group that necessitates the fewest ad hoc assumptions about character transformations is preferred. Monophyletic groups consist of all descendants of a common ancestor, exclusive of any species not descended from that common ancestor. The traditional alternative definitions of monophyly are of such generality as to include all possible combinations of taxa or are dependent on arbitrary taxonomic ranks, or both, and are, therefore, often meaningless in application and information content.

The polarity of character transformation series (plesiomorphy vs apomorphy: primitive vs derived) is determined by outgroup comparison or data from ontogenetic transformations. Outgroup comparisons to characiforms and if necessary other otophysan or ostariophysan groups were used to determine the polarity of characters that vary within the assemblage under examination. The ontogenetic and phylogenetic polarities are considered equivalent for any character that undergoes developmental changes in one of two sister groups. The ontogenetically later stage in the transforming lineage is, therefore, considered apomorphic relative to its homologue in the nontransforming group. This procedure is more parsimonious than assuming that the transition was primitively present in the common ancestor of both groups and was secondarily lost in one lineage (detailed discussions of the theory behind, and methods of application of, the above methodologies can be found in Nelson and Platnick, 1981, and Wiley, 1981).

#### Methods and Materials

Osteological and cartilaginous skeletal systems were examined in cleared and counterstained specimens prepared in a modified version of the alizarin Red S–alcian blue method of Dingerkus and Uhler (1977). Previously cleared specimens stained solely in alizarin Red S, along with dry skeletal materials, were supplemental sources of osteological data. Drawings were reversed into

conventional orientation if drawn from the right side of the specimen. Anatomical illustrations were prepared using a Zeiss microscopic camera lucida. The osteological material and myological preparations examined are deposited in the USNM collections of the National Museum of Natural History, Smithsonian Institution; the American Museum of Natural History (AMNH); and Museo de Biología, Universidad Central de Venezuela (MBUCV). It was impossible to examine each character in all members of the assemblage under discussion given the extremely large number of species involved, the rarity of some nominal forms, and the myriad taxonomic problems in this assemblage. A wide spectrum of genera and species were examined, but it is possible that in some cases the hypothesized distribution of a character may differ from that noted herein.

The following specimens are the basis for illustrations or observations noted in the text. (Measurement in mm is standard length (SL)).

#### CURIMATIDAE

- Curimata cyprinoides* (Linnaeus), USNM 231433; 2 specimens, 17.5–21.7 mm; Surinam, Corantijn River.  
*Curimata vitatta* Kner, USNM 231434; 1 specimen, 81.7 mm; Brazil, Rio Negro (Figures 5, 6, 15–17).  
*Curimatopsis evelynae* Géry, USNM 214794; 4 specimens, 25.7–34.9 mm; Brazil, Rio Negro.  
*Curimatopsis macrolepis* (Steindachner), USNM 231436; 1 specimen, 51.3 mm; Peru.  
*Curimatopsis macrolepis* (Steindachner), USNM 190285; 1 specimen, 34.1 mm; Peru, Iquitos.  
*Potamorhina laticeps* (Valenciennes), USNM 121325; 1 specimen, 129.3 mm; Venezuela, Lake Maracaibo Basin (Figures 1, 2, 25).  
*Potamorhina latior* (Spix), AMNH 48677; 1 specimen, 73.1 mm; Bolivia, Río Mamoré (Figure 27).  
*Psectrogaster amazonica* Eigenmann and Eigenmann, AMNH 40088SD; 1 specimen, 139.2 mm; Bolivia, Río Guaporé (Figures 7, 8, 33, 35).

#### PROCHILODONTIDAE

- Ichthyoelephas* species, USNM 231437; 1 specimen, 110.2 mm; Ecuador (Figures 15, 28).  
*Prochilodus nigricans* Agassiz, USNM 231438; 1 specimen, 144.3 mm; Bolivia, Tumpasa.  
*Prochilodus rubrotaeniatus* Schomburgk, USNM 225419; 1 spec-

- imen, 108.7 mm; Surinam, Corantijn River (Figures 1, 2, 22, 39, 40).  
*Prochilodus* species, USNM 231538; 3 specimens, 29.3–35.2 mm; Amazon River.  
*Semaprochilodus taeniurus* (Steindachner), USNM 231536; 1 specimen, 74.7 mm; Brazil, Rio Negro, vicinity of Manaus (Figure 9).  
*Semaprochilodus taeniurus* (Steindachner), USNM 231537; 1 specimen, 34.7 mm; Brazil, Amazon River.

## ANOSTOMIDAE

- Anostomus plicatus* Eigenmann, USNM 225396; 2 specimens, 75.8–95.3 mm; Surinam, Nickerie District, Matappi Creek.  
*Anostomus* species, USNM 231540; 1 specimen, 81.3 mm; no data (Figures 20, 26).  
*Gnathodolus bidens* Myers, USNM 231539; 1 specimen, 76.2 mm; aquarium material.  
*Laemolyta* species, USNM 179514; 2 specimens, 75.3–77.0 mm; Brazil, Rio Urubu (Figure 11).  
*Leporinus fasciatus* (Bloch), USNM 103847; 1 specimen, 73.2 mm; aquarium material (Figure 29).  
*Leporinus megalepis* Günther, USNM 231541; 1 specimen, 68.2 mm; no data (Figure 23).  
*Leporinus reinhardti* Lutken, AMNH 40104SD; 1 specimen, 170.0 mm; Bolivia, Río Guaporé (Figures 33, 34).  
*Leporinus striatus* Kner, USNM 231948; 26 specimens 68.5–178.5 mm; Colombia, Río Salado (Figure 38).  
*Rhytiodus microlepis* Kner, USNM 163850; 1 specimen, 131.7 mm; Peru, Iquitos.  
*Schizodon fasciatum* Agassiz, USNM 179507; 1 specimen, 49.3 mm; Brazil, Rio Urubu (figures 1, 2, 15).  
*Synaptolaemus cingulatus* Myers and Fernandez-Yepe, MBUCV V-4252; 1 specimen, 71.2 mm; Venezuela, Río Paragua.

## CHILODONTIDAE

- Caenotropus labyrinthicus* (Kner), USNM 231543; 1 specimen, 58.5 mm; Brazil, Rio Negro.  
*Caenotropus labyrinthicus* (Kner), USNM 231544; 1 specimen, 64.2 mm; Venezuela, upper Río Negro (Figure 11).  
*Caenotropus maculosus* (Eigenmann), USNM 231545; 2 specimens, 42.7–46.3 mm; Guyana (Figures 1, 2, 10, 12, 18, 19, 21, 24, 30–32).  
*Caenotropus maculosus* (Eigenmann), USNM 231546; 1 specimen, 97.5 mm; Surinam, Saramaca River.  
*Chilodus punctatus* Müller and Troschel, USNM 231542; 13 specimens, 27.1–38.2 mm; Peru, Río Nanay (Figures 11, 36, 37).

## CHARACIDAE

- Acestrorhynchus falcatus* (Bloch), USNM 225614; 2 specimens, 81.0–85.1 mm; Surinam, Nickerie District, Sisa Creek.  
*Brycon falcatus* Müller and Troschel, USNM 226161; 2 spec-

- imens, 71.3–78.3 mm; Surinam, Corantijn River (Figures 3, 4, 13–15).  
*Carnegiella strigata* (Günther), USNM 225245; 5 specimens, 23.4–25.6 mm; Surinam, Corantijn River.  
*Chalceus macrolepidotus* Cuvier, USNM 231547; 1 specimen, 39.9 mm; aquarium material.  
*Crenuchus spilurus* Günther, USNM 225630; 4 specimens, 21.7–28.2 mm; Surinam, Nickerie District, Lana Creek.  
*Gasteropelecus sternicla* (Linnaeus), USNM 226337; 5 specimens, 29.7–32.5 mm; Surinam, Corantijn River.  
*Hydrolycus pectoralis* (Günther), USNM 231548; 1 specimen, 167.1 mm; Peru, Río Ucayali.  
*Rhaphiodon vulpinus* Agassiz, USNM 231549; 4 specimens, 41.7–44.3 mm; Brazil, Rio Solimões.  
*Salminus maxillosus* Valenciennes, USNM 194213; 1 specimen, 214.7 mm; Venezuela, Río Nitiado-Seco.

## HEMIODONTIDAE

- Anodus elongatus* Spix, USNM 231550; 1 specimen, 120.3 mm; Peru, Río Ucayali.  
*Bivibranchia protractila* Eigenmann, USNM 194363; 1 specimen, 62.8 mm; Brazil, Mato Grosso, upper Rio Jurueña.  
*Hemiodopsis ocellata* Vari, USNM 225593; 1 specimen, 99.6 mm; Surinam, Corantijn River.  
*Hemiodus* species, USNM 231551; 2 specimens, 55.7–57.1 mm; Brazil, Mato Grosso, Rio Arinos.  
*Micromischodus sugillatus* Roberts, USNM 205527; 1 specimen, 96.1 mm; Brazil, Pará.

## PARODONTIDAE

- Parodon suborbitalis* Valenciennes, USNM 231552; 2 specimens, 55.0–58.1 mm; Colombia, Río Salado.  
*Saccodon dariensis* (Meek and Hildebrand), USNM 208505; 1 specimen, 73.3 mm; Panama, Río Membrillo.

## HEPSETIDAE

- Hepsetus odoe* (Bloch), USNM 231553; 1 specimen, 96.2 mm; Togo, Kama.

## CITHARINIDAE

- Citharinus citharus* Geoffroy, USNM 52146; 1 specimen, 218.7 mm; Egypt, Nile River.  
*Citharinus* species, USNM 231554; 2 specimens, 56.3–64.5 mm; Volta, Black Volta River.

## DISTICHODONTIDAE

- Nannocharax intermedius* Boulenger, USNM 231555; 2 specimens, 50.7–63.4 mm; West Africa.  
*Neolebias olbrechtsi* Poll, USNM 227394; 4 specimens, 25.3–29.7 mm; Zaire.  
*Paradistichodus dimidiatus* Pellegrin, USNM 231556; 2 specimens, 45.6–47.3 mm; Ghana, Dayi River.

In addition to the listed specimens, a large number of dry skeletons, stained and cleared glycerine preparations and alcohol preserved specimens in the collections of AMNH and USNM were examined in the comparative studies associated with the present analysis.

**TERMINOLOGY.**—Osteological nomenclature follows Weitzman (1962) with the following modifications. As suggested by Roberts (1969:402), "vomer" is substituted for "prevomer," and "intercalar" for "opisthotic." The element traditionally termed "epihyal" is instead referred to as "posterior ceratohyal." The "ceratohyal" of many previous authors is more correctly termed "anterior ceratohyal." This shift in terminology is a consequence of the lack of serial homology between the so-called epihyal and the epibranchials and the resultant misleading inference of homology inherent in the continued use of "epihyal" (Nelson, 1969:480-481). The use of "epioccipital" rather than "epiotic" follows Patterson (1975). Nelson's substitution (1973) of "angulo-articular" for "articular" and "retroarticular" for "angular" is more reflective of the homologies of these elements among teleosts than previous terminologies and is utilized in this paper. Myological terminology is that of Winterbottom (1974).

Unless noted otherwise, the concepts of the characiform families used in this paper are those of Greenwood et al. (1966) with the following modifications. The Cynodontidae of those authors is considered a tribe in the Characidae rather than a distinct family in keeping with the results of Howes (1976). The Ichthyboridae of Greenwood et al. is placed within the Distichodontidae following Vari (1979:339). The terminology utilized for the major groups of osatriophysan fishes is that of Fink and Fink (1981).

**ABBREVIATIONS.**—The following abbreviations are used in the text and illustrations.

A	division of the adductor mandibulae (1 to 3 and w)
AAP	adductor arcus palatini
AA	angulo-articular
AC	anterior ceratohyal
B	basihyal
BTP	basihyal tooth plate

BB	basibranchial (1 to 4)
BOC	basioccipital
BR	branchiostegal ray
C	ceratobranchial (1 to 5)
CEN	centrum
CL	cleithrum
COR	coracoid
CR	ceratobranchial ridge
CSI	cavum sinus imparis
CTS	connective tissue sheet
DEN	dentary
DH	dorsal hypohyal
DO	dilatator operculi
E	epibranchial (1 to 5)
EAF	efferent artery foramen
ECT	ectopterygoid
EOM	epibranchial organ muscle
EPI	epioccipital
ER	epibranchial ridge
EXT	extrascapular
FR	frontal
FM	foramen magnum
FS	foramen for scaphium
H	hypobranchial (1 to 3)
HA	hyohyoidei abductores
HI	hyohyoidei inferior
HYO	hyomandibula
I	interhyal
INT	interopercle
LAP	levator arcus palatini
LE	lateral ethmoid
LIG	ligament
LOC	lateral occipital foramen
MES	mesopterygoid
MET	metapterygoid
METH	mesethmoid
MX	maxilla
NC	neural canal
NS	neural spine
OP	opercle
OPF	opercular flange
PA	parietal
PAL	palatine
PAP	pterotic articular process
PAR	parasphenoid
PB	infrapharyngobranchial (1 to 4)
PC	posterior ceratohyal
PCL	postcleithrum (1 to 3)
PMX	premaxilla
POST	posttemporal
PP	parapophysis
PR	pleural rib
PRE	preopercle
PTE	pterotic
PZ	prezygapophysis

QUA	quadrate
RA	retroarticular
S	scaphium
SAP	supracleithral articular process
SC	scapula
SCL	supracleithrum
SMX	supramaxilla
SPH	sphenotic
SPO	suprapreopercle
SOP	subopercle
ST	sternohyoideus
SYM	symplectic
UP	upper pharyngeal tooth plate (4 and 5)
V	vomer
VH	ventral hypophyal

### Character Description and Analysis

The phylogenetic analysis of the present study has three primary goals: first, to advance an explicit hypothesis of the phylogenetic relationship of the Curimatidae within the Characiformes; second, to examine the hypothesized monophyly of the Curimatidae and closely related groups; and third, to evaluate the utility of previous alternate classifications as indicators of the phylogenetic history of the Curimatidae and associated lineages.

In this section the characters that show phylogenetically significant variation in the anatomical systems examined in the present study are discussed, along with data that bear on polarity determinations for each character transition series. The evidence from the analyzed characters is brought together in the "Phylogenetic Reconstruction" to advance the most parsimonious hypothesis of the phylogenetic history of the taxa under consideration. The resultant phylogeny serves as the basis for the evaluation of the utility of previously advanced classifications as indicators of phylogenetic relationships among curimatids and closely related taxa (see "Comparisons with Previous Classifications").

The purpose of this study is the advancement of a phylogenetic hypothesis rather than a detailed description of the osteology and soft anatomy of the involved taxa. Thus, only anatomical systems that show variation relevant to the phy-

logenetic reconstruction are discussed. Similarly, only intrafamilial character differences pertinent to the phylogenetic reconstruction at the familial level are detailed. Osteological and soft anatomical systems are discussed separately other than where the functional association between the two systems would make a divided discussion less efficacious.

Among the hypothesized derived characters discovered during the study, a minority were found to have distributions incongruent with the most parsimonious phylogenetic reconstruction based on the overall distribution of synapomorphies. Such homoplasies are recognizable only in the context of the final phylogenetic hypothesis and will be summarized as a group in the "Discussion" section. In order to simplify the evaluation of homoplasies, such characters and their distributional incongruities relative to the arrived at phylogeny will also be discussed at appropriate points in the character descriptions.

### TEETH AND JAWS

The feeding habits of curimatids, prochilodontids, anostomids, and chilodontids range from microphagous filtration of food items from the substrate and water column to micropredation and macrovegetation cropping. The diversity of jaw forms in this assemblage reflects the differing requirements for dealing with that spectrum of food items.

Characiforms most commonly have a single tooth row on the maxilla and one or two rows of moderate-sized teeth on the dentary and premaxilla. The maxilla of chilodontids, curimatids, and anostomids differs from the above pattern in being edentulous throughout ontogeny. The question of the possible presence of maxillary teeth in prochilodontids is difficult to resolve. The prochilodontid suctorial mouth bears multiple rows of numerous small teeth on hypertrophied lips (Roberts, 1973:217). Portions of the dentition overlap the maxilla but are associated with the fleshy lips rather than being attached to the bone itself. Neither phylogenetic nor ontogenetic data

permit a determination of whether the oral disk dentition proximal to the maxilla is homologous with the primitively present maxillary dentition. An assumption of the nonhomology of the multiple tooth rows near the maxilla with the primitive, attached maxillary teeth would make an edentulous maxilla synapomorphic for prochilodontids, anostomids, chilodontids, and curimatids although not unique to these groups among characiforms. Alternatively, it is possible that the oral disk dentition proximal to the prochilodontid maxilla is derived from the plesiomorphous maxillary teeth. If the latter situation approximates the actual phylogenetic history of portions of the prochilodontid oral disk dentition, then the absence of maxillary dentition is not a shared derived character for the four taxon unit but would rather be a synapomorphy for the Anostomidae, Curimatidae, and Chilodontidae. That single character phylogenetic scheme is incongruent with the pattern of relationships considered most parsimonious, based on the overall distribution of all synapomorphies. Within the context of the phylogenetic hypothesis incorporating all examined characters (p. 46), two equally parsimonious explanations could account for the phylogenetic distribution of edentulous maxillae among these taxa. First, the maxillary teeth were independently lost in the ancestral curimatid and the common ancestor of chilodontids and anostomids. Second, maxillary dentition was lost, or already absent, in the common ancestor of the four families but re-acquired in prochilodontids. The conjunction of the uncertain homology of portions of the prochilodontid dentition with questions about character polarity in the system makes it impossible to appropriately use the absence of attached maxillary dentition in the resolution of phylogenetic relationships within the unit that consists of curimatids, prochilodontids, chilodontids, and anostomids.

Departures from the generalized characiform pattern of premaxillary and dentary dentition distinguish each of the families under discussion. Juvenile curimatids (*Curimatopsis macrolepis*, *Curimata cyprinoides*, and various undetermined *Curimata* species) have a single row of attached uni-

cuspidate premaxillary and dentary teeth (see also Géry, 1977b:231). Excepting the absence of maxillary teeth, this dentition pattern agrees in form and distribution with that of various generalized characiforms. Ontogenetically, however, the curimatid premaxilla and dentary undergo a progressive loss of dentition, with adult curimatids being edentulous (Figure 1D). This ontogenetic information and the broad distribution of jaw teeth in characiforms and more inclusive ostariophysan groups indicate that this absence of jaw dentition is derived within characiforms.

Totally edentulous jaws are limited in characiforms to the Curimatidae and the genus *Anodus*, considered by some authors (Eigenmann and Eigenmann, 1889; Fernandez-Yepe, 1948) as a member of that family. Roberts (1974) demonstrated that *Anodus* actually shares numerous derived characters with, and is most closely related to, the Hemiodontidae. The other members of the Hemiodontidae possess well-developed teeth; therefore, the absence of jaw dentition in *Anodus*

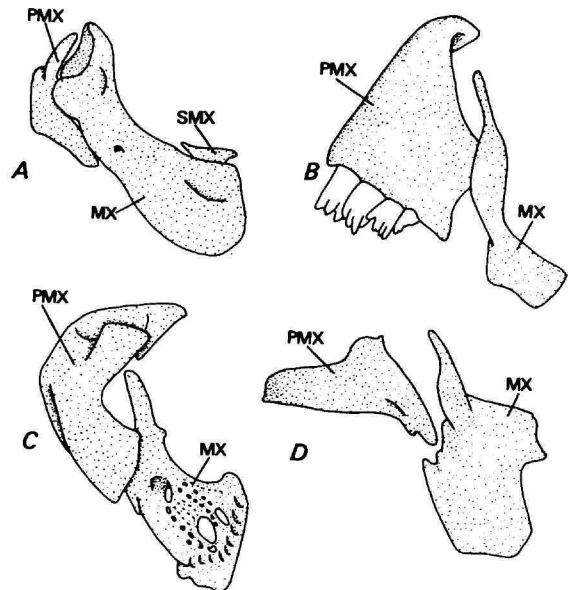


FIGURE 1.—Upper jaws: A, *Caenotropus maculosus*, USNM 231545 (row of reduced teeth not shown); B, *Schizodon fasciatum*, USNM 179507; C, *Prochilodus rubrotaeniatus*, USNM 225419 (multiple rows of reduced teeth not shown); D, *Potamorhina laticeps*, USNM 121325, left side, lateral view.

is most parsimoniously considered a loss achieved independent of that in curimatids.

The teeth of chilodontids and prochilodontids are significantly smaller than those in most characiforms and attach to the fleshy covering of the jaws rather than onto the premaxilla and dentary. The significance of these similarities in these two taxa is difficult to evaluate. Differences in the morphology and distribution of jaw dentition in the two families raise questions as to the homology of the tooth size reduction and the absence of direct tooth to jaw articulation in the lineages. The absence of jaw dentition in adult curimatids could also be considered the terminal state of a transition series whose intermediate stage might have included the precursor of the detached jaw teeth in prochilodontids and chilodontids. Available ontogenetic data does not assist in the evaluation of the preferability of either of these two scenarios. These uncertainties render it impossible to appropriately use the dentition morphology in the Chilodontidae, Prochilodontidae, and Curimatidae for the resolution of phylogenetic relationships in the four-family unit. Neither the hypothesis of the homology of prochilodontid-chilodontid dentitional form nor the hypothesis that considers that condition to be a precursor to the edentulous jaws of curimatids is congruent with the arrived at phylogeny (see "Phylogenetic Reconstruction").

Chilodontids retain the primitive single tooth row on each jaw, whereas prochilodontids have a unique, pronounced increase in the number of functional teeth and replacement tooth rows. Roberts (1973:217) reported about 600 functional teeth in an *Ichthyoelephas* specimen of 97.2 mm SL and 12 replacement tooth rows in larger prochilodontid specimens. That dentition pattern contrasts with a maximum of less than 60 teeth and 2 or 3 replacement tooth rows elsewhere in the order. The pronounced increases in the number of teeth and replacement tooth series are, thus, considered shared derived characters for the members of the Prochilodontidae.

Anostomids retain the single row of premaxillary and dentary teeth common to many characiforms. The teeth of anostomids are, nonetheless,

distinctive in their thickness, multiserrate non-symmetrical cutting edges, increased relative sizes, and the congruent reduction in tooth number (Figure 1B). These shifts from the moderate-sized, more nearly symmetrical, and more numerous teeth that evidently are primitive for the Characiformes are considered synapomorphous for the subunits of the Anostomidae and are very likely correlated with their leaf cropping and micropredatory food habits.

The various distinctive dentitional synapomorphies of the Curimatidae, Prochilodontidae, Chilodontidae, and Anostomidae are reflected in their jaw forms. The overall morphology of the curimatid upper jaw is little altered relative to that of other characiforms (Figure 1D). The derived reduction in the overall strength of the involved bones, the lessening of the medial interconnections between the premaxillae, and the loosening of the articulation between the maxilla and premaxilla are all congruent with the absence of jaw dentition in adult curimatids. These changes are presumably correlated with the lack of firm manipulation of food items by the jaws in this microphagous family.

Unique types of highly derived upper jaws characterize each of the other three families. The chilodontid maxilla (Figure 1A) is greatly enlarged with the well-developed dorsal maxillary process ligamentously attached medially to the mesethmoid's anterolateral surface. The chilodontid premaxilla is small relative to the morphology typical for characiforms and especially so in comparison to the enlarged maxilla in the family. The reduced chilodontid premaxilla forms a limited portion of the upper jaw margin with the paired bones not in contact medially. Rather, the distal portion of the anteroventrally enlarged mesethmoid lies between the premaxillae. In addition to separating those primitively conjoined elements, that portion of the mesethmoid also forms the midsection of the arc of the upper jaw (Figure 32). The dentition associated with the chilodontid upper jaw is reduced in size and not in direct contact with the premaxilla and maxilla, but rather attached to the fleshy lips. The latter modification permits the maintenance

of a continuous row of teeth along the upper jaw despite the intercalation of the mesethmoid between the premaxillae. Chilodontids also have a supernumerary upper jaw ossification: the supramaxilla, situated along the posterodorsal margin of the maxilla (Figure 1A). The association of the robust, enlarged maxilla and a reduced premaxilla is not approximated among characiforms other than chilodontids; neither did outgroup comparisons in that order uncover a mesethmoid that so distinctly separates the premaxillae. A discrete supramaxilla is known elsewhere in the order only in the characid *Chalceus macrolepidotus*. Present concepts on phylogenetic relationships within characiforms indicates that the relationships of *Chalceus* lie with the Neotropical family Characidae, an assemblage that is not an immediate sister group to the Chilodontidae. The common possession of a supramaxilla in *Chalceus* and the Chilodontidae is, therefore, considered to represent two independent acquisitions of that ossification.

The Anostomidae, the hypothesized sister group of the Chilodontidae, has the relative sizes of the upper jaw elements reversed. Anostomids have a very robust, triangular, tooth-bearing premaxilla with a relatively smaller maxilla located along the posteroventral margin of the premaxilla. The overall form of the premaxilla is the result of the apomorphic expansion of the ascending premaxillary process that results in a distinctly triangular element (Figure 1B).

The highly specialized, fleshy suctorial mouth of prochilodontids is supported in part by distinctively structured upper jaw bones (Figure 1C). The outwardly curved premaxilla and maxilla form rounded surfaces which serve as expanded attachment areas for the multilayered fleshy lips that bear the numerous rows of functional and replacement teeth. The pronounced fenestration of the maxilla is especially unusual, with one or more large fenestra along the lateral surface of the element and a number of smaller apertures often arranged in posteroventrally aligned linear series. Neither the outward curvature of the premaxilla and maxilla nor the high degree of fenestration of the latter are found among characi-

forms outside of the family. Equally unusual is the strong bony process that extends posteroventrally from the medial surface of the maxilla. That spur serves as the attachment area for the maxillo-mandibular ligament, which terminates ventrally on the dentary.

Congruent with the modifications of the upper jaw among the four families under discussion are various changes in the form of the lower jaw elements. As in the case of the upper jaw, the mandibular elements in curimatids are the least modified relative to those of most characiforms. The curimatid lower jaw (Figure 2D) is distinguished from the generalized characiform condition primarily in the lack of teeth and tooth associated structures, most notably the dentary replacement tooth trench. The dentary of curimatids is relatively elongate and overlaps the triangular angulo-articular. The retroarticular is a small lateral ossification along the ventral margin of the latter bone. The other three families have the lower jaw foreshortened to differing degrees compared to the relatively elongate mandible of curimatids. Such a foreshortening, although hypothesized to be derived, has a phylogenetic distribution incongruent with the phylogeny arrived at here (p. 46); thereby representing at least two separate trends towards lower-jaw shortening.

The lower jaw of chilodontids is little modified other than in being foreshortened (Figure 2A). The absence in chilodontids of direct contact of the teeth with the dentary is correlated with the absence of a replacement tooth trench. As noted above, that attribute also occurs, evidently independently, in the edentulous curimatids. Anostomids, in contradistinction, have a transversely widened dentary that reflects the expansion of the replacement tooth trench. The widened replacement tooth trench has both an increased attachment area for the enlarged functional teeth (Figure 2B) and space for development of the relatively large replacement dentition. Another unusual aspect of the anostomid dentary replacement tooth trench is the large fenestra on the bone's ventral surface. A total ventral enclosure of the trench is typical for characiforms, and the



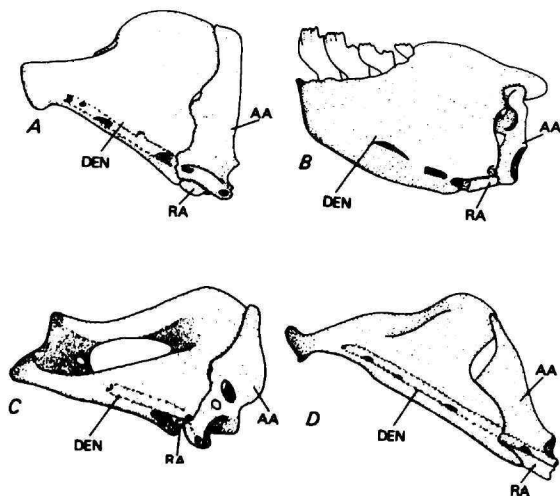


FIGURE 2.—Lower jaws: A, *Caenotropus maculosus*, USNM 231545 (row of reduced teeth not shown); B, *Schizodon fasciatum*, USNM 179507; C, *Prochilodus rubrotaeniatus*, USNM 225419 (multiple rows of reduced teeth not shown); D, *Potamorhina laticeps*, USNM 121325, left side, lateral view.

anostomid form of aperture is not approximated in any other characiform examined for the present study. The anostomid retroarticular lies in a distinct pocket formed by the angulo-articular and dentary (Figure 2B), contrary to the generalized condition in which enclosure by the bordering bones is minimal.

The prochilodontid lower jaw is particularly noteworthy for the alteration of its retroarticular and dentary (Figure 2C). The prochilodontid retroarticular is greatly reduced relative to the typical characiform condition. Equally distinctive is the repositioning of the retroarticular along the anteromedial surface of the angulo-articular, which results in its being barely visible in lateral view. This is a significant shift in size and position from the larger, laterally located retroarticular in other characiforms. The numerous rows of replacement teeth on the lower jaw of prochilodontids are contained in a greatly widened, laterally rotated replacement trench with a large medial fenestra. A rotation of the dentary replacement tooth trench onto the anterior surface of the dentary also characterizes the Citharinidae (Vari, 1979:267). The trench size in that family does not approximate the condition in prochilodontids,

and more inclusive hypotheses of relationships indicate that these rotations in trench position were achieved independently (page 46; Vari, 1979). The medial fenestra opening into the replacement tooth trench in the Prochilodontidae has not been encountered elsewhere in the order.

#### GILL ARCHES

The hypothesized plesiomorphic condition of the characiform gill arches' ventral portion is comparable to that illustrated in Figures 3 and 4. Medially there are three ossified basibranchials, each bordered by paired hypobranchials. The unossified posteriormost fourth basibranchial is an anteriorly wider, overall triangular element. The three pairs of hypobranchials are associated with the first through third basibranchials. The hypobranchials typically are unelaborated, with the exception of hypobranchial 3 which often has an anteroventral, prong-shaped process. When present, that protrusion extends lateral to the ventral aorta and is variously developed in different characiform groups. Ceratobranchials 1 to 3 attach to the lateral margins of the associated hypobranchials, whereas the fourth and fifth ceratobranchials are in direct contact with the unossified fourth basibranchial. The first through third ceratobranchials are elongate, dorsoventrally flattened bones that lack any pronounced dorsal ridges or processes. Ceratobranchial 4 has a comparable overall form and a definite ridge along its ventromedial edge, which serves as the attachment area for a connective tissue band. Ceratobranchial 5 is expanded anteromedially into a flattened, largely horizontal plate, which bears a patch of moderately developed, unicuspidate, dorsally, or posterodorsally directed teeth.

This hypothesized primitive condition of the gill arches among characiforms is modified, often markedly, among members of the families Curimatidae, Prochilodontidae, Anostomidae, and Chilodontidae. The phylogenetic distribution of the various, derived restructurings are congruent with the recognition of the four-taxon assemblage as a natural evolutionary unit and with its division into two monophyletic subunits. One subunit

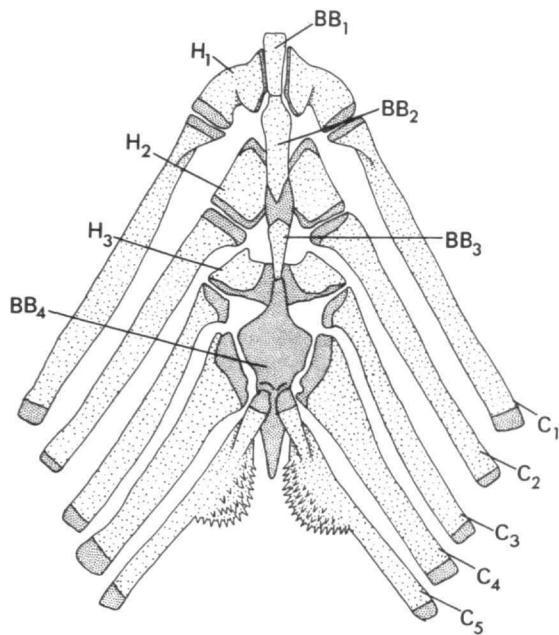


FIGURE 3.—*Brycon falcatus*, USNM 226161, ventral portion of gill arches, dorsal view (denser stippling represents cartilage).

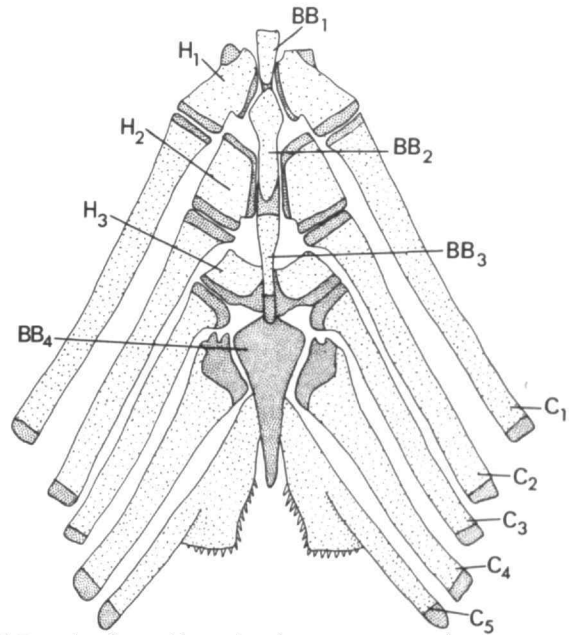


FIGURE 4.—*Brycon falcatus*, USNM 226161, ventral portion of gill arches, ventral view (denser stippling represents cartilage).

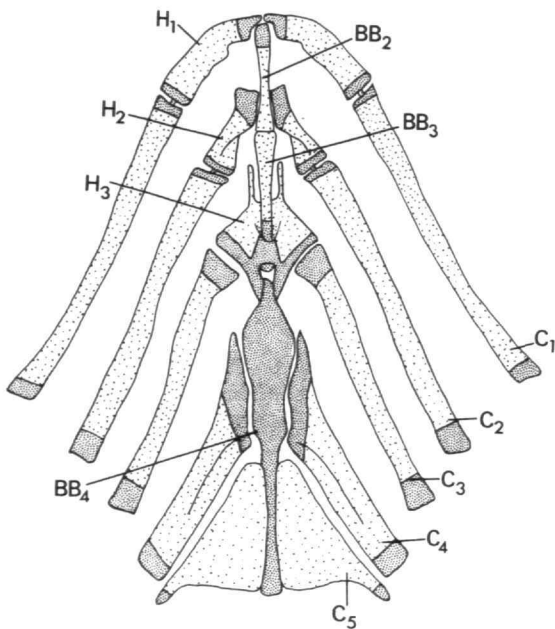


FIGURE 5.—*Curimata vittata*, USNM 231434, ventral portion of gill arches, dorsal view (denser stippling represents cartilage).

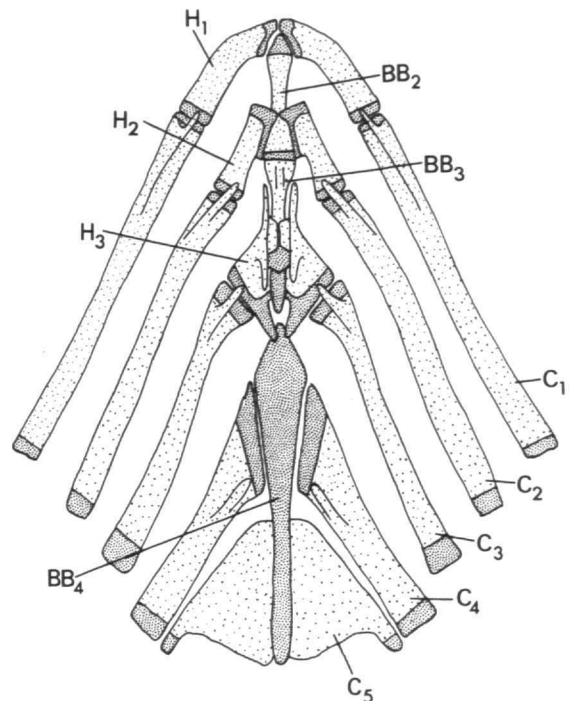


FIGURE 6.—*Curimata vittata*, USNM 231434, ventral portion of gill arches, ventral view (denser stippling represents cartilage).

consists of curimatids and prochilodontids, the other of anostomids and chilodontids.

The most readily apparent difference between the basic form of the ventral portion of the gill arches common to prochilodontids and curimatids and the hypothesized plesiomorphous condition of these elements for characiforms is the marked reduction or absence of dentition on the lower pharyngeal (fifth ceratobranchial) in the adults of these families (Figure 5). Fifth ceratobranchial dentition is present in postlarvae of both families. In specimens of *Prochilodus* of ~ 35 mm SL, six to eight unicuspidate teeth are arranged in two parallel rows along the postero-medial portion of the bone. The progressive ontogenetic loss in lower pharyngeal teeth results in the fifth ceratobranchials of prochilodontids being edentulous in ~ 85 mm SL specimens. Similarly curimatids under ~ 25 mm SL commonly have a patch of unicuspidate teeth on the fifth ceratobranchial. An ontogenetic loss of pharyngeal dentition that leads to toothless fifth ceratobranchials is common to the vast majority of curimatid species, particularly those that attain an adult standard length over 50 mm. In some of the smaller species, however, the reduction is not carried to its ultimate limit. Fully grown *Curimatopsis* species (i.e., ~ 25 mm SL) retain a distinct, albeit greatly reduced, patch of teeth on the fifth ceratobranchial.

Within the Characiformes a reduction or elimination of lower pharyngeal dentition also occurs in the Neotropical genus *Anodus* (Roberts, 1974:223) and the African family Citharinidae (Vari, 1979:303). Various shared derived characters unite these taxa respectively to the Hemiodontidae (Roberts, 1974) and Distichodontidae (Vari, 1979). The latter families otherwise have a full complement of lower pharyngeal dentition. The reduction or elimination of fifth ceratobranchial dentition in *Anodus* and the Citharinidae is consequently most parsimoniously considered a homoplasy relative to the comparable adaptation common to curimatids and prochilodontids.

The lower portion of the gill arches also provides some other phylogenetically interesting characters. A prominent, anteriorly directed pro-

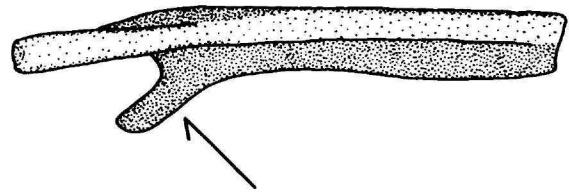


FIGURE 7.—*Psectrogaster amazonica*, AMNH 40088SD, ceratobranchial 4, left side, lateral view (arrow points to ventral process).

cess extends from the fourth ceratobranchial's anteromedial surface in prochilodontids and curimatids (Figures 6, 7). This process is an apomorphic elaboration of the ridge on the medial portion of the fourth ceratobranchial in other characiforms. In a similar fashion the anterior corner of the third hypobranchial is often antero-ventrally prolonged in characiforms into a prong-shaped process that extends lateral to the ventral aorta. Curimatids have the ventral portion of that process apomorphously further expanded ventrally and posteriorly to form a vertical wall that extends lateral to, and evidently partially supports, the ventral aorta (Figures 6, 8). Anterior and posterior extensions of this process' ventral margin are positioned along the lateral wall of the blood vessel. The degree of development of these secondary processes vary among different subunits of the family.

Certain hemiodontids (*Anodus*, *Hemiodus*, *Hemiodopsis* (Vari, 1982a:191), *Micromischodus* and *Bivibranchia*) and chilodontids (*Caenotropus*) also have prominent ventral processes of the third

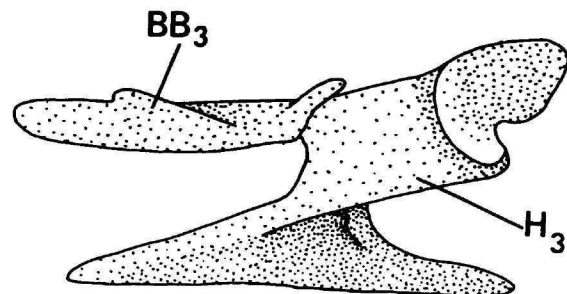


FIGURE 8.—*Psectrogaster amazonica*, AMNH 40088SD, basi-branchial 3 and hypobranchial 3, left side, lateral view, showing ventral process of hypobranchial 3.

hypobranchial. The hypobranchial projections in those taxa arise from the ventrolateral margin of the main body of the hypobranchial rather than the ventromedial portion of the element as in curimatids. Those structures are consequently considered nonhomologous with the adaptations in the latter family; a hypothesis congruent with the arrived at hypothesis of relationships.

The first basibranchial is the final phylogenetically significant character discovered in the ventral portion of the gill arches in curimatids and prochilodontids. Most characiforms have a relatively well-developed conical or elongate first basibranchial that extends distinctly anterior to the first hypobranchial (Figures 3, 10). In prochilodontids, however, basibranchial 1 is a small, triangular element approximate to the anterior margin of basibranchial 2 and barely extends anteriorly to the level of the anterior terminus of the first hypobranchial (Figure 9). This reductional trend is carried further in the Curimatidae, which lack a separate, ossified first basibranchial (Figure 5). Available evidence does not permit a decision as to whether the conical cartilagenous process anterior to the ossified second basibranchial of curimatids represents the unossified remnant of

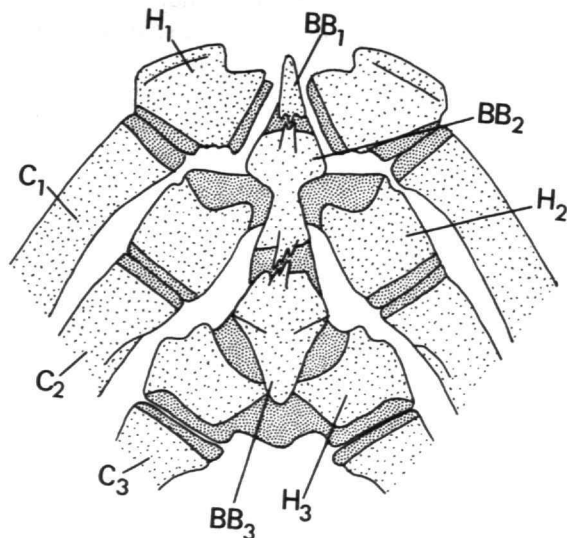


FIGURE 9.—*Semaprochilodus taeniurus*, USNM 231536, ventral portion of gill arches, anterior region, dorsal view (denser stippling represents cartilage).

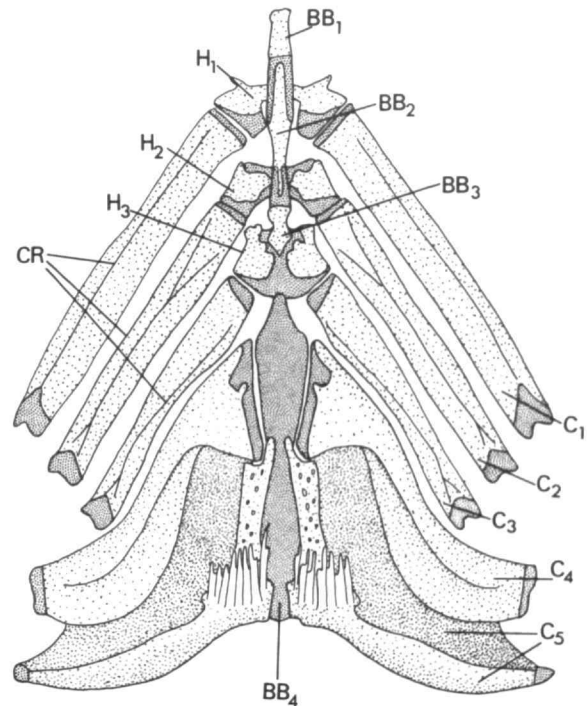


FIGURE 10.—*Caenotropus maculosus*, USNM 231545, ventral portion of gill arches, dorsal view (denser stippling represents cartilage).

the reduced first basibranchial of prochilodontids. Nonetheless, an ossified first basibranchial is widespread in otophysans and its reduction and ultimate loss are, thus, considered synapomorphies of different levels of universality within the prochilodontid-curimatid lineage. The lack of an unossified first basibranchial also occurs homoplasiously in the examined adults of at least some anostomids (*Rhytiodus microlepis*, *Pseudanos irinae* (Winterbottom, 1980:40)) and parodontids (*Parodon suborbitalis*).

The primary shared derived character for anostomids and chilodontids in the gill arches' ventral portion involves the fifth ceratobranchial dentition (Figure 10). Chilodontids and anostomids have enlarged bi- or multicuspitate teeth rather than the relatively small or moderately developed unicuspidate pharyngeal dentition common to most characiforms. Bicuspidate pharyngeal teeth with unequally developed cusps are

universal among anostomids (Figure 11A). The elaboration of the distal portion of the fifth ceratobranchial dentition progresses further in *Caenotropus* and *Chilodus* in which the lower pharyngeal teeth have three cusps of markedly different size aligned along the longitudinal body axis. This dentition is comparable to that of the upper portions of the *Caenotropus* gill arches, as illustrated in Figure 11B.

Lower pharyngeal dentition enlarged to the degree found in chilodontids and anostomids has not been reported or observed elsewhere among characiforms (Roberts, 1969:424; Winterbottom, 1980:2). Consequently, its possession is most appropriately considered a shared derived character. Non-unicuspidate pharyngeal dentition is known to occur in only one other characiform, the hemiodontid *Bivibranchia*, which has tricuspidate teeth on the fifth ceratobranchial (Roberts, 1974, fig. 37). The equally developed, transversely or obliquely transversely oriented, tooth cusps of *Bivibranchia* do not appear to be homologous with the anteroposteriorly oriented cusps of markedly different size found in chilodontids and anostomids. Furthermore, as discussed by Roberts, *Bivibranchia* is evidently most closely related to hemiodontids, a family otherwise characterized by unicuspidate pharyngeal teeth. The anatomical and phylogenetic data concordantly indicate that the tricuspidate dentition of *Bivibranchia* is a homoplasy relative to the apomorphous bi- or multicuspidate tooth forms common to the Chilodontidae and Anostomidae.

Although numerous fish groups with prominent epibranchial organs have associated alterations of the gill arches' dorsal portion, chilodontids are unusual, if not unique, in also incorporating elements of the ventral portion of the

FIGURE 11.—Form of fifth upper pharyngeal tooth plate dentition, left side, lateral view: A, *Laemolyta* species, USNM 179514; B, *Caenotropus labyrinthicus*, USNM 231544; C, *Chilodus punctatus*, USNM 231542. (Scale = 0.1 mm.)

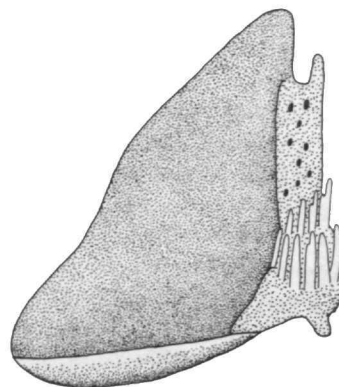
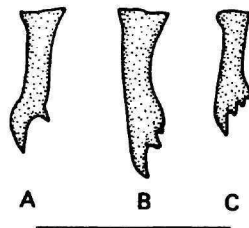


FIGURE 12.—*Caenotropus maculosus*, USNM 231545, fifth ceratobranchial, left side, dorsal view.

branchial apparatus into the system. Most notable are the modifications of the fourth and fifth ceratobranchials. The enlarged fourth ceratobranchial (Figures 10, 21) has greatly expanded posterior and posteroventral surfaces that form a broad curved plate which closely approximates neighboring portions of the enlarged fifth ceratobranchial (Figures 10, 12, 21). The increased size and modified form of the fourth ceratobranchial are seemingly unique to chilodontids among ostariophysans. The lower pharyngeal (fifth ceratobranchial) of chilodontids is similarly totally restructured (Figures 10, 12) relative to the condition basic for characiforms (Figure 3). Most distinctive is the great expansion of the ventral portion of ceratobranchial 5 into a broad, cup-shaped plate that extends under and closely approximates the posterior and ventral surfaces of the enlarged fourth ceratobranchial (Figures 10, 21). Dorsomedially the fifth ceratobranchial is a flattened, fenestrated plate that extends anteriorly along the dorsal surface of the cartilagenous fourth basibranchial. Posteriorly the tooth-bearing portion of the bone is expanded dorsally and rotated anteriorly. This results in the associated dentition being oriented directly anteriorly or having only a slight dorsal inclination contrary to the plesiomorphous dorsal or moderately anterodorsal orientation of these teeth in other characiforms. The chilodontid gill arches also have prominent dorsal ridges that arise from the main

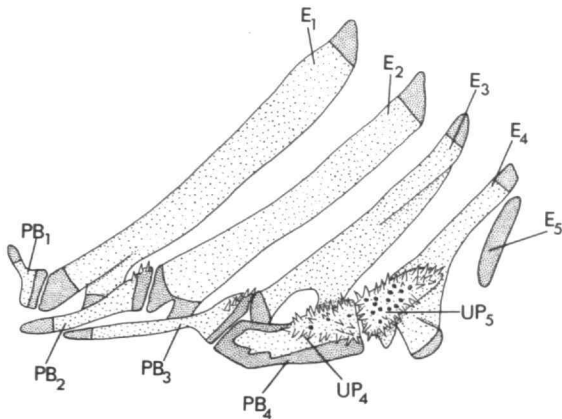


FIGURE 13.—*Brycon falcatus*, USNM 226161, dorsal portion of gill arches, left side, ventral view (denser stippling represents cartilage).

body of ceratobranchials 1, 2, and 3 (Figure 10). Such elaborations are distinctive relative to the primitive, flattened dorsal surface of these elements in other characiforms. Whether, and how, these ridges are functionally related to the epibranchial organs is unknown. Ceratobranchial ridges also occur in the hemiodontid *Bivibranchia*. In that genus the margins of the ridges are straight and the main body of the entire ceratobranchial is bowed ventrally; a system different from the chilodontid form of ceratobranchial ridge. Furthermore, *Bivibranchia* apparently is not closely related to the assemblage formed by chilodontids and anostomids. The conjunction of these factors leads to an assumption that the ceratobranchial elaborations in *Bivibranchia* and the Chilodontidae are homoplasious.

Characiforms as a whole more typically demonstrate alterations of the gill arches' dorsal portion than restructurings of the branchial apparatus' ventral region. This dichotomy is apparent among curimatids, prochilodontids, anostomids, and chilodontids, all of which have some of the most pronounced alterations of the dorsal portions of the gill arches among characiforms. Once again some modifications are synapomorphic for the four-family unit, while others delineate two subgroups within the assemblage. The first subgroup consists of the Curimatidae and Pro-

chilodontidae and the second of the Anostomidae and Chilodontidae.

The hypothesized plesiomorphous characiform morphology of the gill arches' dorsal portion is comparable to that illustrated for *Brycon* (Figures 13, 14). Four infrapharyngobranchials occur along the midline. The first, a small, rod-like or triangular element associated with the first epibranchial, is ligamentously attached dorsally to the neurocranium. Infrapharyngobranchials 2 and 3 are triangular, anteriorly directed elements that contact their respective epibranchials laterally. The fourth infrapharyngobranchial is a flattened cartilage that extends between the third infrapharyngobranchial and the fourth epibranchial. Epibranchials 1 through 3 are elongate, flattened structures unelaborated other than for proximal uncinete processes. The fourth epibranchial is a more complex triangular bone with a well-developed, dorsally directed process above the fifth upper pharyngeal tooth plate. Posterolaterally, the fourth epibranchial articulates with the relatively small, rod-shaped, cartilaginous fifth epibranchial (Figures 13–15). The fourth and fifth epibranchials diverge dorsally, with an intervening groove that serves as the passage for the fifth efferent branchial artery. Upper pharyngeal tooth plate 4 is attached to the ventral surface of the fourth infrapharyngobranchial,

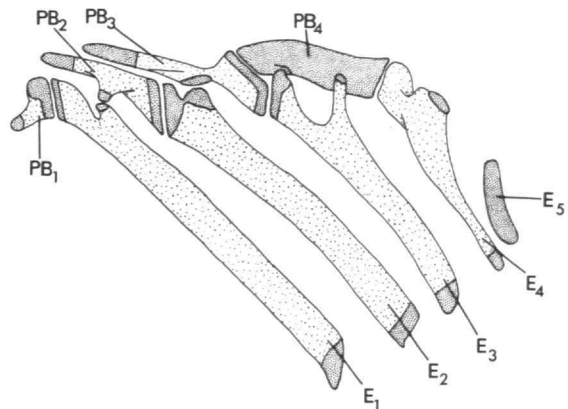


FIGURE 14.—*Brycon falcatus*, USNM 226161, dorsal portion of gill arches, left side, dorsal view (denser stippling represents cartilage).

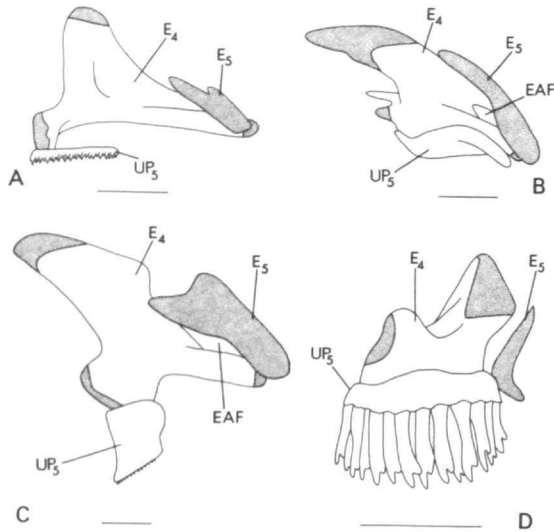


FIGURE 15.—Fourth and fifth epibranchials, fifth upper pharyngeal tooth plate, and associated dentition, right side, medial view: A, *Brycon falcatus*, USNM 226161; B, *Curimata vittata*, USNM 231434; C, *Ichthyoelephas* species, USNM 231437; D, *Schizodon fasciatum*, USNM 179507. (Scales = 1.0 mm; stippling represents cartilage).

while upper pharyngeal tooth plate 5 is joined dorsally to the fourth epibranchial's ventral section. The two tooth plates together form a continuous, flattened bony sheet that bears a patch of small unicuspidate teeth, which oppose those on the fifth ceratobranchial. Comparable small unicuspidate dentition often also occurs in small patches on the ventral surfaces of the second and third infrapharyngobranchials.

Curimatids, prochilodontids, anostomids, and chilodontids have in common a pronounced reduction in the amount and distribution of pharyngeal dentition. Most notable is their lack of teeth on the fourth upper pharyngeal tooth plate ( $UP_4$ ), a condition here considered to be derived within characiforms relative to the previously described presumed primitive condition. Reduced or absent dentition on the fourth upper pharyngeal tooth plate is not unique to this particular assemblage within the order. Among Old World characiforms, an edentulous  $UP_4$  occurs in all citharinids and in some, but not all, species of the distichodontid genera *Hemigrammocharax*, *Nan-*

*nocharax* and *Neolebias* (Vari, 1979:303–305). Reduced dentition on the fourth upper pharyngeal tooth plate also characterizes the Neotropical hemiodontid genus *Anodus*. Although derived, the reduction or loss of dentition on the fourth upper pharyngeal tooth plate does not delimit a natural assemblage. The species of *Hemigrammocharax*, *Nannocharax*, and *Neolebias* that have reduced dentition on the fourth upper pharyngeal tooth plate are all relatively small forms with congruent reductions in the overall ossification of other head parts. Furthermore, the data on relationships within and between these distichodontid genera make it most parsimonious to conclude that this loss of dentition was achieved independently in each lineage and that a complete pattern of pharyngeal dentition was ancestral for distichodontids (Vari, 1979:305). The citharinids *Citharidium* and *Citharinus*, which also lack teeth on the fourth upper pharyngeal tooth plate, are hypothesized to form the sister assemblage to the Distichodontidae (Vari, 1979:324). The presence of dentition on the fourth upper pharyngeal tooth plate in characiform outgroups and most members of the Distichodontidae indicates that the edentulous nature of the element in citharinids, although most simply considered a synapomorphy for the members of that family, is a homoplasy relative to the comparable condition in curimatids, prochilodontids, anostomids, and chilodontids. A number of derived characters place *Anodus*, in which  $UP_4$  lacks teeth, within the Hemiodontidae (Roberts, 1974:429). The remaining members of that family have the more typical plesiomorphic characiform pattern of complete pharyngeal dentition, which is consequently considered the primitive condition for the Hemiodontidae.

Curimatids, prochilodontids, anostomids, and chilodontids or subunits of that assemblage share restructurings of the fourth upper pharyngeal tooth plate. All four families lack the plesiomorphic close contact of the fourth and fifth upper pharyngeal tooth plates (Figures 16–19). The absence of that immediate association of those elements is thus hypothesized to be a shared derived character for the quadrifamilial grouping. Curimatids and prochilodontids have a somewhat

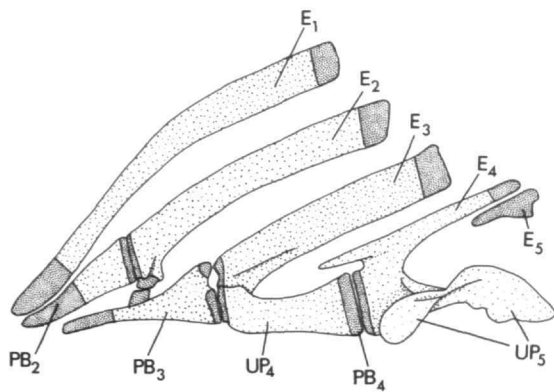


FIGURE 16.—*Curimata vittata*, USNM 231434, dorsal portion of gill arches, left side, ventral view (denser stippling represents cartilage).

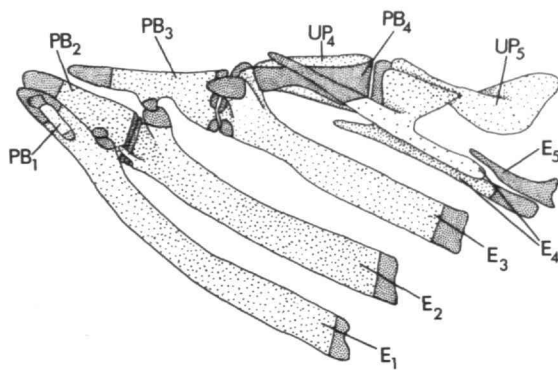


FIGURE 17.—*Curimata vittata*, USNM 231434, dorsal portion of gill arches, left side, dorsal view (denser stippling represents cartilage).

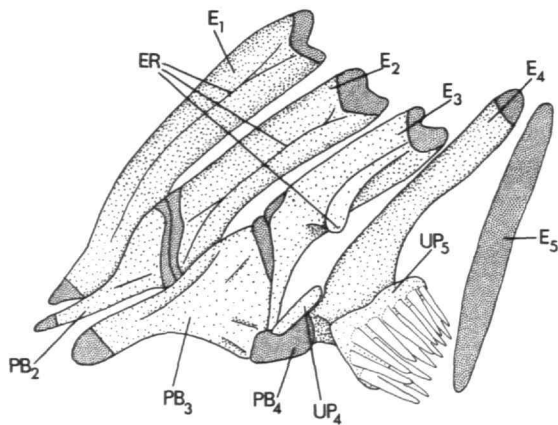


FIGURE 18.—*Caenotropus maculosus*, USNM 231545, dorsal portion of gill arches, left side, ventral view (denser stippling represents cartilage).

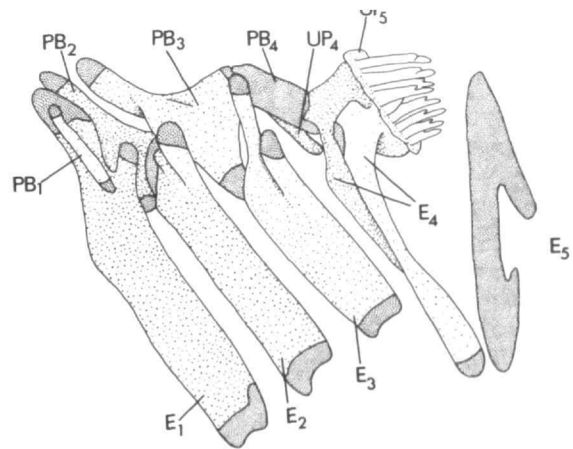


FIGURE 19.—*Caenotropus maculosus*, USNM 231545, dorsal portion of gill arches, left side, dorsal view (denser stippling represents cartilage).

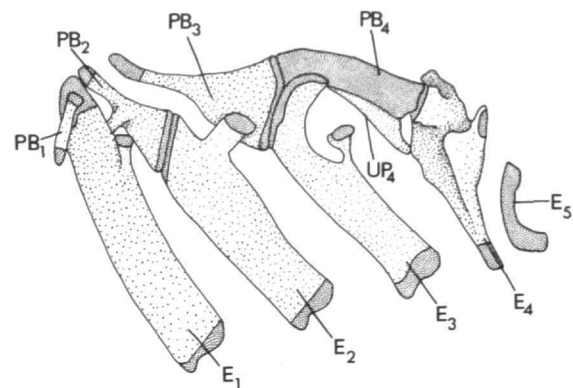


FIGURE 20.—*Anostomus* species, USNM 231540, dorsal portion of gill arches, left side, dorsal view (denser stippling represents cartilage).

reduced fourth upper pharyngeal tooth plate that no longer retains its primitive direct contact posteriorly with the elements of the fifth gill arch (Figure 16). In addition to its separation from the fifth upper pharyngeal tooth plate, UP<sub>4</sub> is also apomorphously altered into a curved sheet that surrounds the ventral, lateral, and sometimes portions of the dorsal surfaces of the fourth infra-pharyngobranchial (Figures 16, 17); a marked shift from the flat tooth plate form typical for characiforms. Anostomids and chilodontids retain the flattened form of the fourth upper pha-



ryngeal tooth plate hypothesized to be primitive but have the posterior portion of the element shifted laterally (Figure 18). Consequently, the posterior portion of UP<sub>4</sub> now contacts the anterolateral surface of the main body of the fourth epibranchial rather than the anterior margin of the fifth upper pharyngeal tooth plate. The marked reorientation of the tooth plate apparent in anostomids is more pronounced in chilodontids.

Subunits of the four-family assemblage under consideration have the form of the fifth upper pharyngeal tooth plate (UP<sub>5</sub>) modified in different ways relative to the hypothesized plesiomorphous flattened plate common to most characiforms. Prochilodontids have a transversely compressed fifth upper pharyngeal tooth plate movably articulated with the fourth epibranchial (Figure 15c; Roberts, 1974, fig. 22). In the Anostomidae and Chilodontidae the fifth upper pharyngeal tooth plate is vertically thickened relative to the condition generalized for characiforms. Among chilodontids, this thickened plate is additionally rotated posterodorsally. As a consequence, the primitively ventral surface of UP<sub>5</sub> is oriented to face posteriorly (Figures 18, 19). The various restructurings of the fifth upper pharyngeal tooth plate in prochilodontids, anostomids, and chilodontids are not known to occur elsewhere among characiforms. Therefore, they are considered derived characters of differing levels of universality. In the Curimatidae, UP<sub>5</sub> is apomorphously expanded posteriorly and posteroventrally into a curved, somewhat convoluted ossification (Figures 15B, 16) that contacts and matches the curved dorsal surface of the fifth ceratobranchial. A posterior extension of UP<sub>5</sub> somewhat comparable to that in curimatids occurs in the Old World citharinids (Vari, 1979, fig. 28). The pronounced difference in the morphology of the bony plates in the two families and the overall distribution of derived characters within characiforms indicates that these are analogous rather than homologous changes.

Distinctive modifications of the fifth upper pharyngeal tooth plate dentition distinguish subunits of the four-family assemblage. Prochilodontids have reduced teeth with swollen bases on

that element (Roberts, 1973, fig. 22). Comparable teeth occur at some point in the ontogeny of various curimatids. The majority of curimatid species have carried the trend towards tooth reduction further and have very few teeth on the fifth upper pharyngeal tooth plate, or have an edentulous bone. Roberts (1973:219) reported that "in Curimatidae third and fourth epibranchial and fifth ceratobranchial toothplates bear numerous conical teeth . . ." Observations associated with the present study have shown, however, that curimatids are characterized by the marked reduction or absence of teeth on the fifth upper pharyngeal tooth plate, the absence of teeth on the fifth ceratobranchial, and an edentulous fourth upper pharyngeal tooth plate. Elsewhere among characiforms, a reduction in the UP<sub>5</sub> dentition comparable to that in curimatids is known only in the Old World family Citharinidae (Vari, 1979:303). However, numerous synapomorphies unite the Curimatidae to the Prochilodontidae (see "Phylogenetic Reconstruction") and various derived characters indicate that the Citharinidae forms the sister group to the Distichodontidae (Vari, 1979:324). Given those more inclusive hypotheses of relationship, it is simplest to consider the edentulous nature of the fifth upper pharyngeal tooth plate in citharinids to be a homoplasy relative to the reduced dentition on that bone in curimatids. This convergent reduction in the UP<sub>5</sub> dentition in the microphagous curimatids and citharinids may be a consequence of the decreased utility of pharyngeal teeth in fishes with that feeding habit. The congruent, hypothesized homoplasious expansion of the fifth upper pharyngeal tooth plate is possibly associated with the food concentrating function of the epibranchial organs.

The enlarged bi- or multicuspidate dentition on the fifth upper pharyngeal tooth plate of anostomids and chilodontids is comparable to that on the fifth ceratobranchial. Anostomids have totally bicuspidate pharyngeal dentition (Figures 11A, 15D). *Caenotropus* (family Chilodontidae) has tricuspidate pharyngeal teeth on both ventral and dorsal portions of the gill arches (Figure 11B). The dentition on the fifth upper pharyngeal tooth plate of *Chilodus* (Chilodonti-

dae) is quadricuspidate (Figure 11c) and opposes the tricuspidate teeth on the fifth ceratobranchial. Enlarged non-unicuspidate  $UP_5$  dentition is limited to the preceding families among characiforms examined, with the single exception of the hemiodontid *Bivibranchia* (Roberts, 1974, fig. 37). As in the case of the lower pharyngeal dentition, the supernumerary tooth cusps on the teeth in the upper portion of the gill arches in this hemiodontid are evidently nonhomologous with those of anostomids and chilodontids.

An overall restructuring of many other elements in the dorsal portions of the gill arches occurs in anostomids and chilodontids. The form of the anteromedial process of the third epibranchial of anostomids is distinctive among characiforms. This transversely widened portion of the bone has a distinct process that is somewhat dorsally recurved, thereby extending over the dorsal surface of the fourth infrapharyngobranchial (Figure 20). The third infrapharyngobranchial of anostomids and chilodontids is transversely widened posteriorly relative to the plesiomorphous characiform condition. This expansion is most pronounced in chilodontids (Figures 18, 19), in which the associated third epibranchial has an elongate slender medial process that extends dorsally to the fourth infrapharyngobranchial. Chilodontids have pronounced ridges on the ventral surfaces of epibranchial 1, 2, and 3 that oppose the dorsal ridges on the three anteriormost ceratobranchials (Figure 18). Most highly developed is the process on epibranchial 3. Once again the ridge form in the Chilodontidae differs in detail from that of the hemiodontid *Bivibranchia*. The anatomical differences and the data associating *Bivibranchia* phylogenetically with the Hemiodontidae (Roberts, 1974) indicate that the ridges in that genus and the Chilodontidae are evidently analogous rather than homologous elaborations of the involved ceratobranchials.

Epibranchial 4 is notably modified in the Curimatidae, Prochilodontidae, Anostomidae, and Chilodontidae. In curimatids and prochilodontids, the primitively dorsally directed process of the fourth epibranchial (the dorsal extension of

Nelson (1967) and the suprpharyngobranchial process of Bertmar et al. (1969)) is expanded and reoriented anteriorly, thereby extending over the dorsal surface of the fourth infrapharyngobranchial (Figures 15B,C, 17). The resultant sheet of bone and cartilage runs parallel to, and is closely associated with, the lateral surface of the pharyngeal outpocketing of the epibranchial organ. This vertical plate in these taxa is also extended posteriorly and posterodorsally by a significant anterodorsal expansion of the cartilaginous fifth epibranchial, which attaches to the rear of the fourth epibranchial (Figures 15B,C). The enlarged form of the cartilage contrasts with the usual characiform condition of a relatively small fifth epibranchial dorsally separated from the fourth. The dorsal contact between the fourth and fifth epibranchials in curimatids and prochilodontids results in the encirclement of fifth efferent branchial artery. Comparable expansions of the fourth and fifth epibranchials with a resultant enclosure of the efferent artery are associated with well-developed epibranchial organs in various fish groups (Nelson, 1967:76, 83). However, other than curimatids and prochilodontids, no characiform with well-developed epibranchial organs is known to have such an association of these elements.

In anostomids (Figure 15D) and chilodontids, the form of the fourth epibranchial is dramatically altered relative to the condition hypothesized to be plesiomorphous for characiforms. The dorsal process of the bone in these families is considerably thickened transversely and foreshortened longitudinally. Furthermore, the primary axis of the process also has a posterodorsal alignment rather than the dorsal or anterodorsal orientation that characterizes other characiforms. The anterior portion of the fourth epibranchial, which articulates with the cartilaginous fourth infrapharyngobranchial, has undergone a considerable vertical expansion in anostomids and chilodontids. That expanded portion of the bone and the posteriorly reoriented dorsal process delimit a distinct, transversely aligned notch along the dorsal surface of the bone (Figures 15D, 19, 20). The notch serves as an attachment area for the

very large obliquus dorsalis muscle that extends anteriorly to the fourth infrapharyngobranchial. In no other characiform examined has such a highly developed form of this upper pharyngeal muscle been found. The alteration of the overall form of the fourth epibranchial is carried further in chilodontids (Figures 18, 19), which have the ventromedial surface of that element rotated posterodorsally. As a consequence the dentition on the associated fifth upper pharyngeal tooth plate points posteroventrally rather than ventrally as in other characiforms.

Chilodontids also have a number of modifications of the upper portions of the gill arches that are associated with their unique form of epibranchial organ.

#### EPIBRANCHIAL ORGANS

Epibranchial organs have been reported in a number of fish groups including clupeoids, osteoglossiforms, and ostariophysans. Within the Ostariophysa (sensu Rosen and Greenwood, 1970, and Fink and Fink, 1981), such a system is known in some gonorhynchiforms, characiforms, and cypriniforms. The typical teleostean epibranchial organ is primarily associated with the fourth epibranchial and consists of paired dorsal diverticuli of the branchial chamber. Each diverticulum communicates posteroventrally with the pharynx via an aperture in the posterodorsal region of the branchial chamber. Most early students studying the system suggested that the epibranchial organs in characiforms had a respiratory function (e.g., Sagemehl, 1887; Rauther, 1910). Subsequent research by Heim (1935) on the Old World characiforms *Distichodus* (Distichodontidae) and *Citharinus* (Citharinidae) and the New World genera *Curimatus* (Curimatidae) and *Prochilodus* (Prochilodontidae), followed by Anglescu and Gneri's (1949) research on *Prochilodus* and Bertmar's study (1961) on *Citharinus* indicate that epibranchial organs in the examined taxa are not accessories of the respiratory system. Rather they serve to sense food items in, and concentrate them from, the water column and/or substrate (see Bertmar et al., 1969, for a detailed discussion).

Moderately developed pharyngeal outpocketings associated with the fourth and fifth epibranchials have been reported in some African characids and distichodontids (Daget, 1958, 1959, 1960; Bertmar, 1961:156). Highly developed epibranchial organs, however, are present within the suborder only in the African Citharinidae (Sagemehl, 1885, 1887; Daget, 1962a, 1962b) and the Neotropical Chilodontidae, Prochilodontidae, and Curimatidae (Kner, 1861; Heim, 1935) (for Hemiodontidae, see p. 22). Although well-developed epibranchial organs are hypothesized to be derived for characiforms, they apparently are not a shared derived character for all the taxa possessing them. Pronounced differences between the three types of highly developed epibranchial organs in the group cast doubt on the homology of these adaptations, as do present concepts of higher level phylogenetic relationships among characiforms.

The epibranchial organ in the citharinids *Citharidium* and *Citharinus* is an elaborate system of foliate lobes and dichotomously branching internal tubes supported by numerous bony spicules (Daget, 1962a, figs. 6-8). Epibranchial organs of that type are presently unknown elsewhere among teleostean fishes (Bertmar et al., 1969, table 1). This unique anatomy suggests that the citharinid epibranchial organ is a synapomorphy for the members of that family, analogous rather than homologous with the well-developed pharyngeal diverticuli in some other characiforms. That hypothesis is congruent with more inclusive concepts of relationships based on shared derived characters and the lack or poor development of epibranchial diverticuli in distichodontids, the hypothesized sister group to citharinids (see Vari, 1979:322, for a further discussion).

The epibranchial organs of curimatids and prochilodontids are elongate, longitudinally aligned sacs with both longitudinal and circular muscles in their walls (Heim, 1935:64, 71). Commencing at the posterodorsal limits of the branchial chamber, the diverticuli then extend dorsally and anterodorsally over the fourth infrapharyngobranchial, the fourth and fifth upper pharyngeal tooth plates, and part of the tooth epibranchial. The

medial surfaces of the sacs are in contact or slightly separated, with each diverticulum enclosed laterally by the enlarged cartilaginous fifth epibranchial and anteriorly expanded osseous and cartilaginous dorsal process of the fourth epibranchial. Although Bertmar et al. (1969:20) state that the hemiodontid *Hemiodus* and the chilodontid *Caenotropus* have large, sac-like epibranchial diverticuli, the present study has not found such pharyngeal outpocketings in those genera. The only hemiodontid with a noticeable posterodorsal epibranchial pouch is *Anodus*, which was not placed in the Hemiodontidae at the time of the study by Bertmar et al. The diverticulum in *Anodus* is relatively small outpocketing at the posterodorsal limit of the branchial apparatus and is formed largely by a cartilage associated with the fifth ceratobranchial. It, furthermore, does not extend dorsal of the fourth epibranchial and fourth infrapharyngobranchial. The *Anodus* pharyngeal diverticulum thus differs in both position and structure relative to the sac-like, muscular, dorsally located epibranchial organs of curimatids and prochilodontids; the two forms of diverticuli are consequently considered nonhomologous.

The cited presence of sac-like epibranchial organs in *Caenotropus* is a misinterpretation of the system in that genus. The pharyngeal diverticulum of chilodontids, including *Caenotropus*, is composed largely of cartilage and connective tissue sheets and differs in numerous details from that of curimatids and prochilodontids. Those differences and available data on phylogenetic relationships of chilodontids support the hypothesis that the pharyngeal diverticulum in the Chilodontidae is nonhomologous with the sac-like muscular epibranchial organ of some other characiforms. Thus, the sac-like epibranchial organ form of the Curimatidae and Prochilodontidae is apparently synapomorphously limited to those families among characiforms, with the reports by Bertmar et al. (1969) of large sac-like epibranchial organs in the Hemiodontidae and Chilodontidae being evidently erroneous.

The final highly developed epibranchial organ form within the Characiformes is common to all

chilodontids. Bertmar et al. (1969:20) erroneously considered the epibranchial organ of the chilodontid *Caenotropus* to be equivalent to the expanded, sac-like epibranchial organs of curimatids and prochilodontids. They also described the epibranchial organ of the chilodontid *Microdus* as "more convoluted and heliciform . . . than that of other characoids." As alluded to above, the epibranchial organ of *Caenotropus* is nonhomologous with that in curimatids and prochilodontids. Rather it is like that described by Bertmar et al. for *Microdus*, which is an older, although preoccupied, generic name for species now placed in *Caenotropus* (Géry, 1964:6).

Several features of the chilodontid epibranchial organ are unknown among other characiform groups. Foremost among these are the restructurings of the fourth and fifth ceratobranchials and their incorporation into the epibranchial organ system (see "Gill Arches"). The exact functional significance of the expansion of the apparatus into the ventral portions of the gill arches is uncertain. However, the adjoining surfaces of the expanded ceratobranchials form two broadly curved, matching plates (Figures 10, 21) with the adjacent surfaces in close contact and covered by sheets of smooth connective tissue. Laterally this covering layer is developed into a series of radially arranged, interdigitating ridges (Géry, 1964, fig. 2), which presumably filter food particles from the water passed from the oral cavity.

The dorsal portions of the epibranchial organs also incorporate atypical elements. The posterodorsal margin of the fifth ceratobranchial is joined to a broad, shell-shaped connective tissue sheet (Figure 21). That structure extends upward above the level of the dorsal portions of the epibranchials and forms the posterior wall of a partially helical, medially spiraling epibranchial chamber. The anterior wall of the transversely oriented chamber is largely formed by the cartilaginous fifth epibranchial, which is significantly expanded vertically and transversely relative to the condition in other characiforms (Figure 21). The fifth epibranchial's ventral margin is attached by a connective tissue sheet to the posteroventral margin of the fourth epibranchial. That

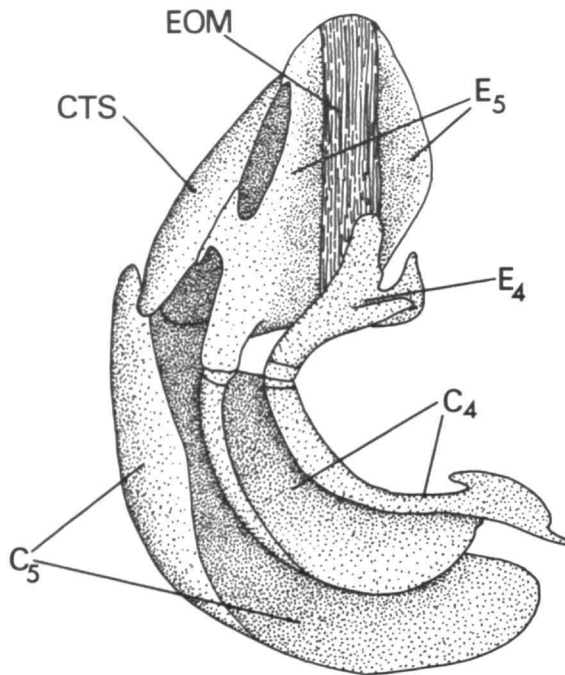


FIGURE 21.—*Caenotropus maculosus*, USNM 231545, fourth and fifth branchial arches and anterior portion of epibranchial organ muscle, right side, anterolateral view.

common connective tissue band then continues ventrally to attach to the fourth ceratobranchial's dorsolateral surface. This soft tissue complex interconnects the dorsal cul-de-sac with the space delimited by the expanded fourth and fifth ceratobranchials; an association between the dorsal and ventral portions of the branchial apparatus limited to chilodontids among fishes.

Chilodontids lack the circular and longitudinal musculature found in the sac-like epibranchial organs of curimatids and prochilodontids. Rather their epibranchial organs are formed largely of nonmuscular tissue with only a single, narrow, vertical muscle band that extends along the external surface of the anterior and posterior walls of the epibranchial portion of the diverticulum (Figure 21). The muscle segment on the anterior face of the epibranchial organ arises from the primitively dorsal surface of the fourth epibranchial. It extends dorsally from its origin to pass over the upper edge of the fifth epibranchial and

joins its counterpart on the posterodorsal surface of the epibranchial organ. The posterior portion of the muscle band arises in part on the posteroventral margin of the fifth ceratobranchial and partially on the posterior surface of the shell-shaped connective tissue band surmounting that bone. The anterior and posterior muscle bundles join on the posterior surface of the epibranchial organ slightly ventral to the dorsal border of the epibranchial organ. The resultant common muscle band extends dorsally from this point of contact to insert on the neurocranium. Although the exact homology of these epibranchial organ muscles is uncertain, they are considered a synapomorphy for all chilodontids because of the lack of any comparable musculature in the branchial apparatus of other characiforms.

The concurrent presence in chilodontids of well-developed pharyngeal dentition and large epibranchial organs runs counter to the general pattern noted by Nelson (1967:81), in which the development of large epibranchial diverticuli is typically accompanied by a reduction or elimination of pharyngeal dentition. The functional significance of the association of such seemingly disparate adaptations—a large epibranchial organ correlated with filter-feeding and enlarged pharyngeal teeth usually associated with shredding of larger food items—is unknown. An in-depth examination of food habits in the group may resolve the question.

The possession of epibranchial organs has been hypothesized to be the ancestral condition for various groups of fishes by Bertmar et al. (1969:44). They consequently suggested that the absence of these adaptations in members of various lineages was achieved by repeated independent losses. Nelson (1967), in contrast, advanced the suggestion that the presence of such epibranchial diverticuli in different groups of fishes represented independent acquisitions and that the absence of these pharyngeal outpocketings constituted the ancestral state for teleostean fishes. The scope of this study is too limited to analyze which of these hypotheses is most parsimonious for all subunits of the Teleostei. However, the morphology of well-developed epibranchial or-

gans in characiforms indicates that the three forms of the diverticuli in chilodontids, citharinids, and the unit formed by curimatids and prochilodontids are analogous, homoplasious developments. The hypothesis that these diverticuli arose independently in each lineage is also the most parsimonious within the context of our present knowledge of relationships within the Characiformes. Similarly, the epibranchial organ in the cyprinid *Hypophthalmichthys* is an analog of the various systems in characiforms, with that genus most closely related to other cyprinids that lack the adaptation (Howes, 1981). Comparable arguments apply to the pharyngeal diverticuli of various gonorrhynchiformes. Therefore, the anatomical and phylogenetic evidence concordantly indicates that, for the Ostariophysi, the hypothesis that large epibranchial organs are apomorphous independent acquisitions as stated by Nelson, is more parsimonious than the hypothesis of Bertmar et al., who considered such outpocketings ancestral for all teleosts.

#### HYOID APPARATUS

The four families under discussion possess a series of hyoid arch alterations congruent with adaptations of other portions of the oral apparatus. The generalized and presumed plesiomorphic hyoid arch form for characiforms is comparable to that in *Brycon* (Weitzman, 1962, fig. 11c). The arch's lateral portion consists of ventral and dorsal hypohyals followed posteriorly by anterior and posterior ceratohyals. The hypohyals are transversely wide, complex bones, whereas the ceratohyals are distinctly compressed, laterally unelaborated elements. The anterior ceratohyal is approximately twice as long as the posterior (e.g., *Prochilodus*, Figure 22). The hyoid series is completed posterodorsally by a rod-like interhyal, which attaches ligamentously to the dorsal surface of the posterior ceratohyal (e.g., *Leporinus*, Figure 23). In the majority of characiforms the basihyal is a relatively elongate element, ossified approximate to the hypohyals and cartilaginous anteriorly. The ossified and cartilaginous portions of the element are both partially overlain dorsally

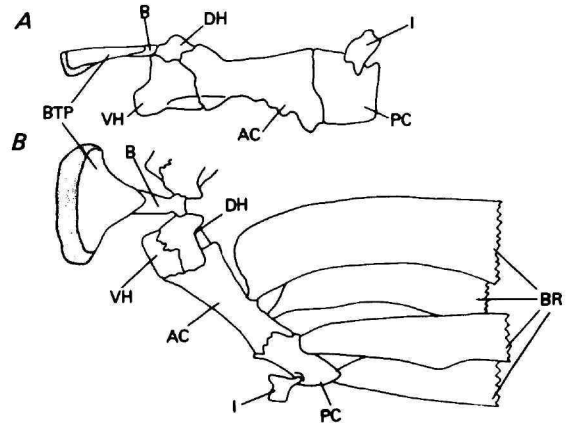


FIGURE 22.—*Prochilodus rubrotaeniatus*, USNM 225419, hyoid arch: A, left side, lateral view (branchiostegal rays removed); B, left side, dorsal view. (Stippling represents cartilage.)

by the edentulous basihyal tooth plate (e.g., *Leporinus*, Figure 23). Four branchiostegal rays are common to most characiforms, three attached to the anterior ceratohyal and one to the posterior. The relative width of these elements is variable within the order, but the degree of overlap between neighboring rays is usually not extensive. The median urohyal typically has a moderately developed laminar vertical process and horizontal lateral wings.

The hyoid arches of curimatids differ from those just described only in the lateral expansion of the anterior portions of the basihyal and basihyal tooth plate, which results in a distinctly triangular basihyal complex. The anterolateral expansion of these elements is carried further in prochilodontids (Figure 22b) in which the anterior margin of the complex is apomorphously greatly developed transversely. This enlargement progresses ontogenetically to result in a squat T-shaped basihyal complex in larger individuals. Several other alterations of the hyoid arches characterize the Prochilodontidae. Smaller individuals of the family have a distinctive ventrally notched interhyal straddling a corresponding depression in the dorsal surface of the posterior ceratohyal (Roberts, 1973:219). Large specimens that were examined have the interhyal notch less pronounced, but there is often (always?) a distinct sesamoid cartilage in the ligament that joins the

interhyal to the posterior ceratohyal. Neither an equivalent interhyal form nor a comparable independent ossification in the ligament have been encountered in the characiform outgroups examined. Prochilodontids also have a marked broadening of the branchiostegal rays, particularly the most lateral element, and a unique form of urohyal with highly developed, laterally directed ventral wings. Once again these apomorphic modifications are not found in curimatids, anostomids, and chilodontids, but are present, evidently as homoplasies, in some distichodontids (*Nannocharax*) and parodontids (*Parodon*).

The overall hyoid arch form of anostomids and chilodontids is unique within characiforms. Singularly notable is the longitudinal foreshortening and transverse expansion of the lateral portions of the system (compare Figures 23 and 24 with 22). Anostomids and chilodontids also share a posteroventrally slanting joint between the anterior and posterior ceratohyals. The degree of obliqueness differs significantly within anostomids, but a distinctly nonvertical joint is by far the most common condition in both families. Most other characiforms have a vertical articulation between these elements. However, an oblique area of contact between these elements occurs sporadically in some other characiform groups,

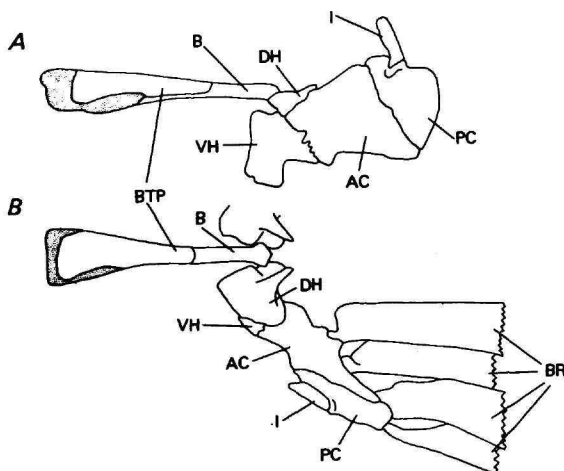


FIGURE 23.—*Leporinus megalopsis*, USNM 231541, hyoid arch: A, left side, lateral view (branchiostegal rays removed); B, left side, dorsal view. (Stippling represents cartilage.)

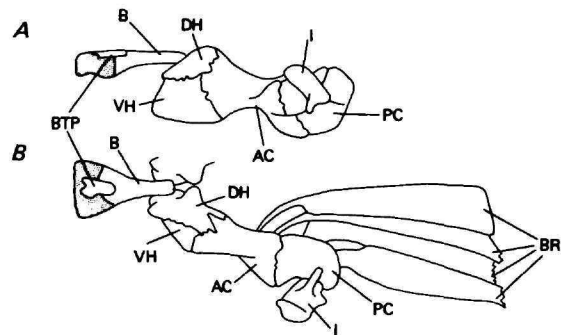


FIGURE 24.—*Caenotropus maculosus*, USNM 231545, hyoid arch: A, left side, lateral view (branchiostegal rays removed); B, left side, dorsal view. (Stippling represents cartilage.)

most notably in a subunit of the Distichodontidae (e.g., *Paradistichodus*), in which it was apparently achieved independently.

The thickening of the lateral elements in the hyoid arch, particularly the anterior and posterior ceratohyals, is most pronounced in the Chilodontidae. Another notable feature of the hyoid arch of that family is the prominent horizontal ridge extending from the posterior portion of the anterior ceratohyal onto the adjoining region of the posterior ceratohyal. Chilodontids also have a thickened, complex interhyal with a distinct medial process that extends onto a depression on the dorsomedial surface of the posterior ceratohyal. This process serves as the point of attachment for the ligament that joins the interhyal to the metapterygoid and quadrate. Such an attachment is a pronounced shift from the usual insertion of the ligament on the dorsal portion of the main body of the interhyal and is not known in the other characiform groups examined. This medial process of chilodontids is somewhat similar to the medial portion of the ventrally notched prochilodontid interhyal. However, the ligamentous attachments of the interhyal in prochilodontids are of the type generalized for characiforms rather than comparable to those of chilodontids.

#### SUSPENSORIUM AND CIRCUMORBITAL SERIES

Many of the derived characters in the suspensorium of curimatids, prochilodontids, anostomids, and chilodontids are associated with trophic

specializations. Functionally, the majority of these modifications are related either to differing degrees of mobility between the suspensorium and neurocranium or to relative motion of subunits of the suspensory apparatus. Two distinctive suspensorium modifications, one in curimatids and the other in anostomids involve the relationship of the suspensorium and the neurocranium and serve to further reduce mobility between those systems.

Characiforms typically have a single, anterodorsal articular surface on the palatine. This cartilagenous portion of the bone contacts both the vomerine region of the neurocranium anterodorsally and the cartilage associated with the upper arm of the maxilla laterally (the submaxillary cartilage of Daget (1964, fig. 23) and ethmopalatine cartilage of Fink and Fink (1981:311)). The palatine in curimatids is apomorphously expanded posterodorsally to form a second, cartilage-topped articular surface. That cap of cartilage is continuous ventrolaterally with the relatively thick cartilaginous mass that overlies the lateral portions of the metapterygoid and ectopterygoid (Figure 25). A corresponding cartilage-capped articular process formed by an anterovent-

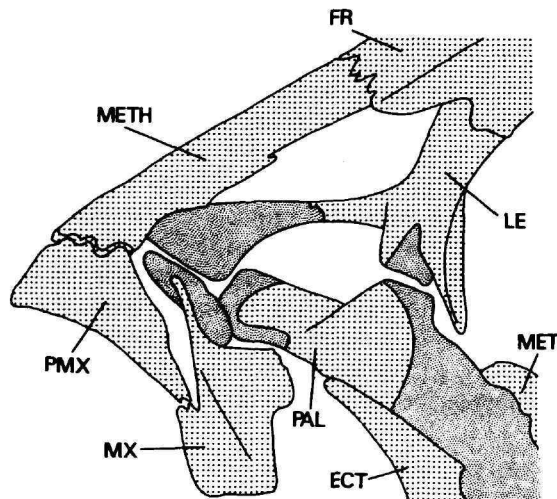


FIGURE 25.—*Potamorhina laticeps*, USNM 121325, upper jaw and anterior portion of suspensorium and neurocranium, left side, lateral view (denser stippling represents cartilage).

tral expansion of the distal margin of the lateral ethmoid's ventral wing contacts the palatine's posterodorsal process (Figure 25). Although derived for characiforms, a close articulation of the lateral ethmoid and palatine, per se, is not unique to curimatids within the order. Various forms of contact between those elements are also found in the Old World hepsetid characiform *Hepsetus* and in the Neotropical characid genera *Salminus*, *Acestrotrhynchus*, *Rhaphiodon*, *Hydrolycus*, and *Crenuchus*. The *Hepsetus* lateral ethmoid-palatine joint differs from that in curimatids in having two distinct contact points between the bones. Furthermore, the lateral ethmoid's anterior process serves as the point of articulation rather than the bone's ventral wing as in curimatids. The section of the palatine that contacts the lateral ethmoid in *Salminus* is a posterior extension of the originally anterodorsal articular surface of the bone, a situation also not comparable to that in curimatids. The common possession of various derived characters (e.g., presence of an ossified rhinosphenoid) indicates that *Acestrotrhynchus*, *Rhaphiodon*, and *Hydrolycus* are most closely related to taxa that lack any lateral ethmoid-palatine contact. Therefore, it is most parsimonious to consider the presence of the articulation in those noncurimatid genera as homoplasious relative to the condition in the Curimatidae; a hypothesis also congruent with the distribution of shared derived characters that unite the Curimatidae and its close relatives (see "Phylogenetic Reconstruction").

The form of the lateral ethmoid-palatine contact in curimatids and the characid genus *Crenuchus* does not differ notably. However, *Crenuchus* has a median orbital ossification which may represent an autapomorphous form of rhinosphenoid. If correct, that homology would support the hypothesis that *Crenuchus* is more closely related to characiforms with a rhinosphenoid than to those, such as curimatids, that lack it. Rhinosphenoid-bearing taxa generally lack the secondary palatine joint. Therefore, if the median orbital ossification of *Crenuchus* is homologous to the rhinosphenoid, the secondary palatine joint of that genus would be presumed homoplasious relative to the articulation in curimatids. In the absence



of a homology between the median orbital ossification of *Crenuchus* and the rhinosphenoid, it can, nonetheless, be noted that *Crenuchus* lacks the numerous synapomorphies shared by curimatids and their close relatives. That situation is incongruent with the union of curimatids and *Crenuchus* in a monophyletic assemblage as would be suggested by their common possession of indistinguishable forms of lateral ethmoid-palatine joints. Under either alternative the lateral ethmoid-palatine articulations in curimatids and *Crenuchus* (and perhaps its close relatives) are most parsimoniously considered independent acquisitions.

In anostomids and chilodontids the contact between the suspensorium and lateral ethmoid is tightened by an alternate system. Chilodontids have a discrete cord-like ligamentous band that arises from the unelaborated dorsolateral surface of the ectopterygoid. That connective tissue band extends posterodorsally lateral to the palatine and attaches to the anteroventral surface of the lateral ethmoid's ventral wing. Anostomids have the modifications carried further (Figures 26, 38). In

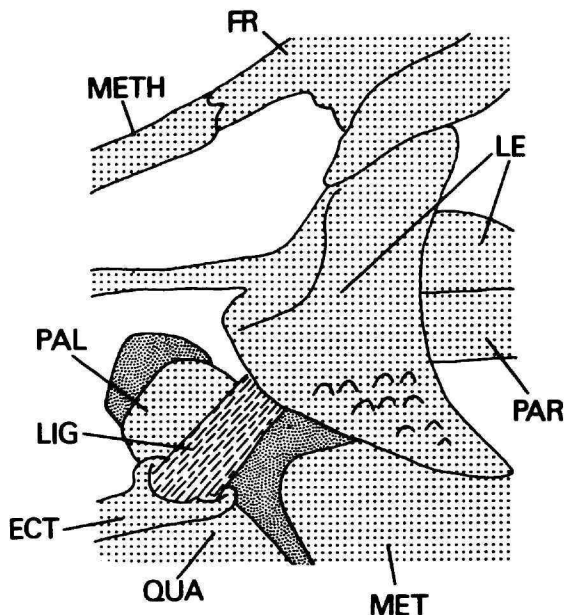


FIGURE 26.—*Anostomus* species, USNM 231540, lateral ethmoid and anterodorsal portion of suspensorium, left side, lateral view (denser stippling represents cartilage).

most members of that family a well-developed lateral process on the posterodorsal portion of the ectopterygoid serves as the attachment point for a cord-like ligament both thicker and stronger than that in chilodontids. As in chilodontids, the ligament passes lateral to the palatine, but rather than terminating on the anteroventral margin of the lateral ethmoid's ventral process, it attaches in a pit-like depression on the anteroventral portion of the bone.

A broad connective tissue sheet between the neurocranium, particularly the parasphenoid, and the medial and dorsal margins of at least the metapterygoid and mesopterygoid portions of the suspensorium is ubiquitous among characiforms. In some members of the order, portions of the connective tissue sheet are thickened into one or more cord- or strap-like ligamentous bands that join the medial margins of the suspensorium to the vomer or adjoining areas (e.g., prochilodontids and some curimatids). However, examination of characiform outgroups has not revealed taxa other than anostomids and chilodontids with a thick ligament that extends between the suspensorium's lateral surface and the lateral ethmoid. The presence of some form of discrete lateral ethmoid-ectopterygoid ligament is, therefore, considered a shared derived character for chilodontids and anostomids. The posterolateral process on the ectopterygoid, which serves as an attachment point of the ligament, and the thickening of that connective tissue band are further elaborations of the system synapomorphic for the members of the Anostomidae.

No traces of an ectopterygoid process or the associated ligamentous band are found in the anostomid *Gnathodolus*, contrary to the broad distribution of those characters in anostomids. In *Gnathodolus*, the elongate, horizontally aligned ectopterygoid is very distant from the lateral ethmoid and is flexibly attached to the dorsal margin of the quadrate (Winterbottom, 1980, figs. 41, 58). The primary function of the lateral ethmoid-ectopterygoid ligament in other anostomids appears to be in reducing motion between the neurocranium and suspensorium. The wide separation of the ectopterygoid from the lateral ethmoid

and its mobility relative to the quadrate would drastically diminish, if not eliminate, the stabilizing action of the ligament in *Gnathodolus*. The absence of the connective tissue band and of the associated ectopterygoid modifications is consequently not unexpected from a functional viewpoint. As noted, the ligamentous attachment is present in chilodontids, the sister group of the Anostomidae. Furthermore, the other anostomids examined, perhaps including *Synaptolaemus* the sister genus to the lineage containing *Gnathodolus* (Winterbottom, 1980), have the lateral elaboration of the ectopterygoid and an ectopterygoid-lateral ethmoid ligament. (A definite statement on the presence or absence of the ligament in *Synaptolaemus* cannot be made based on available material, but the dorsolateral process on the ectopterygoid is present, although not prominent.) The lack of the ligament in *Gnathodolus* (and perhaps its sister genus *Sartor*) is most parsimoniously considered a secondary loss rather than the primitive absence of the band given the presence of the ligament in sister groups to *Gnathodolus* of increasing universality.

The preceding discussion has dealt with modifications that involve the functional relationship of the suspensorium with the neurocranium. A number of other characters are found in subunits of the suspensorium. Curimatids have the least modified form of suspensorium (Figure 27) among the four families that are the primary focus of this study. Nonetheless, they have several derived alterations of the system, including the secondary articular facet on the palatine discussed above. Curimatids are also distinguished by a horizontal shelf along the dorsomedial surface of the metapterygoid and sometimes mesopterygoid (Figure 27b). This evidently apomorphic elaboration of the metapterygoid does not occur in the family's close relatives. The somewhat similar horizontal shelf on the medial surface of the metapterygoid described by Winterbottom (1980:50) in various anostomids is formed by the ventral bending of the dorsal margin of the metapterygoid rather than via an elaboration of the medial surface of that element.

Roberts (1974:429) used the presence of a strong, posteroventrally sloping flange located on

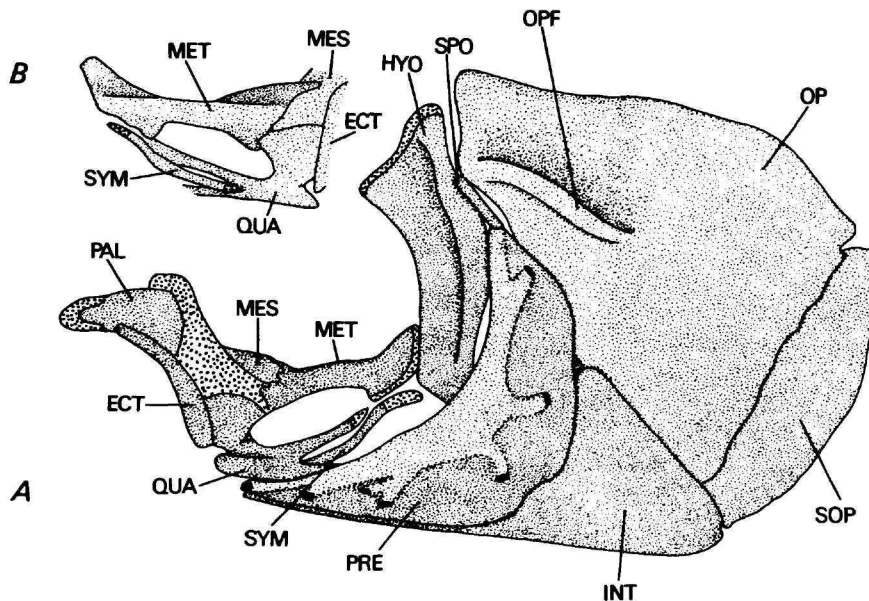


FIGURE 27.—*Potamorhina latior*, AMNH 48677: A, suspensorium, left side, lateral view; B, detail of region of metapterygoid-quadrate fenestra, left side, medial view.

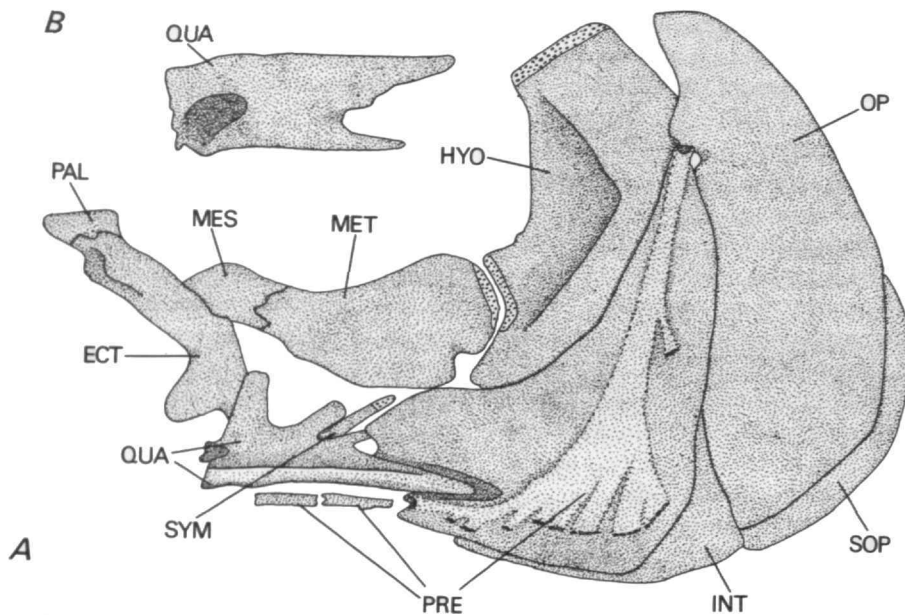


FIGURE 28.—*Ichthyoelephas* species, USNM 231437: A, suspensorium, left side, lateral view; B, quadrate, left side, ventral view.

the opercle's lateral surface just above the hyomandibula-opercle joint in the Curimatidae as a distinguishing feature of that family (Figure 27). In an earlier paper Roberts (1973:213) rejected previous hypotheses of a close relationship of curimatids and prochilodontids, citing in support of his argument the absence of an opercular flange in prochilodontids, among other differences. Such an absence would, in and of itself, be actually irrelevant to the question of the interfamilial relationships since, if unique to curimatids, the flange would be a synapomorphy for the members of that family with no bearing on the question of curimatid-prochilodontid relationships. That point is moot, however, since prochilodontid juveniles have an opercular flange identical to that in curimatids. The prochilodontid flange undergoes a unique ontogenetic modification that leads to the condition Roberts equated with the plesiomorphous, laterally unelaborated opercle. Juvenile prochilodontids of ~ 20 to 40 mm SL have a posteroventrally slanting, dorsally undercut opercular flange. With increasing body size, the members of the family develop a series

of bony ridges that extend posterodorsally at approximately right angles from the main body of the process. Although similar secondary processes also occur in larger adult curimatids, in prochilodontids the processes' number and degree of development increases ontogenetically, leading to a progressive masking of the originally discrete flange. The flange is still apparent in ~ 80 mm SL specimens but indistinguishable in individuals of over 100 mm SL in which the ridges have coalesced into a gently sloping, thickened area on the opercle's lateral surface. In large specimens the thickening is not apparent in lateral view (Figure 28A), but it is readily visible when the bone is examined in transmitted light. The opercular modifications of curimatids and prochilodontids presumably serve to strengthen the opercle in these microphagous fishes that use a suctorial feeding mode that requires the movement of relatively large water volumes through the oral chamber. These characters are derived at two levels of universality. The presence of an opercular flange or a further derived condition of that process is synapomorphic for the Curima-

tidae and the Prochilodontidae, while the further elaboration of the flange is a shared derived character for the members of the Prochilodontidae. A distinct opercular flange also characterizes the African characiform family Citharindae (Vari, 1979:295), which also consists of microphagous filter feeders. However, the flange in that taxon differs in several features from the process in curimatids and juvenile prochilodontids. Furthermore, citharinids share numerous, often unique, synapomorphies with, and are evidently most closely related to, distichodontids, which lack a lateral elaboration of the opercle. Thus, the opercular flange of the African family is considered homoplasious with respect to that in the Curimatidae and Prochilodontidae.

The prochilodontid "suctorial" mouth is unique among characiforms with its functional modifications reflected in the numerous changes in the form and relationships of the elements of the suspensorium's anterior portion. Roberts (1974) has previously discussed the osteology of prochilodontids, and it is only necessary to review the adaptations of phylogenetic interest. In lateral view the prochilodontid ectopterygoid is tripartite, with a definite anteroventral process (Figure 28A) that contrasts with the relatively straight margin of the ectopterygoid in most characiforms. Equally distinctive is the high mobility of the ectopterygoid that results from its loose ligamentous attachments to the quadrate and mesopterygoid. Ectopterygoid-quadrate mobility is also present in hemiodontids and parodontids. However, the relationships of the involved elements in those taxa differ from the condition in prochilodontids, and neither family has the ectopterygoid-mesopterygoid mobility characteristic of prochilodontids. Roberts (1973:218) also reported ectopterygoid-quadrate mobility in the Anostomidae. The anostomids on which that observation was based were not specifically noted, although *Schizodon fasciatus* and an unidentified *Leporinus* species are figured or cited in the text. However, the ectopterygoid and quadrate are tightly, immovably joined in the *Schizodon* and *Leporinus* material examined in the present study. Indeed, the only anostomid studied with a mobile ectopterygoid-

quadrate joint is the highly specialized *Gnathodolus*, in which the ectopterygoid is shifted away from the anterior margin of the remaining elements of the pterygoid series. Reference to the reconstruction of anostomin phylogeny arrived at by Winterbottom (1980) shows that *Gnathodolus* is a member of a lineage whose sister species, *Synaptolaemus cingulatus*, lacks ectopterygoid-quadrate mobility. That concept of relationships in conjunction with the immobile contact of these elements in other anostomids results in the most parsimonious hypothesis: *Gnathodolus* achieved ectopterygoid-quadrate mobility independently of prochilodontids.

Pronounced quadrate-preopercle mobility is another character unique to prochilodontids in the Characiformes. The prochilodontid quadrate is laterally expanded into a prominent horizontal shelf that serves as an expanded attachment area for portions of the adductor mandibulae muscles. Medially the quadrate has a comparable, though less pronounced process that extends along the inner surface of the preopercle (Figure 28B). The horizontal notch delimited by the medial and lateral quadrate processes fits into the corresponding vertical notch bordered by dorsal and ventral subdivisions of the preopercle's anterior portion (Figure 28). This distinctive joint permits significant vertical motion of the quadrate on the preopercle. A prominent lateral quadrate shelf also occurs among characiforms in chilodontids and anostomids. The phylogenetic hypotheses of relationships arrived at in this study indicate, however, that these three families do not form a monophyletic group (see "Phylogenetic Reconstruction") but that, rather, prochilodontids are more closely related to curimatids than to the unit that consists of anostomids and chilodontids. Within that hypothesis of relationships there exist two equally parsimonious explanations for the distribution of this derived character. First, that the quadrate shelf arose in the common ancestor of the four families and was secondarily eliminated in curimatids. Second, that the quadrate shelf was independently acquired in the ancestor of the Prochilodontidae and in the common ancestor of the Anostomidae and Chilodontidae.

Anostomids have further expanded the attachment area for the adductor musculature via a lateral shelf on the preopercle's ventral arm. That process forms part of the floor of the bony trough whose lateral wall is the posterolateral process of the quadrate. The preopercular shelf continues posteriorly beyond the terminus of the quadrate in the form of a gradually diminishing ridge. Although not unique to anostomids, a well-developed lateral preopercular shelf is considered derived within characiforms. A comparable preopercular elaboration also occurs in a subunit of the Distichodontidae (Vari, 1979:293). The distichodontid subunit that has the preopercular expansion is evidently most closely related to other members of that family, which lack a laterally elaborated preopercle. The Distichodontidae, in turn, shares a variety of derived characters with the Citharinidae in which the preopercular shelf is also absent. Thus, the presence of the preopercular shelf in some distichodontids is evidently an independent acquisition relative to the process in anostomids.

Anostomids and prochilodontids may share two other derived suspensorium characters. Several questions exist, however, on the homology of

the modifications in the two taxa. A preopercle with an enclosed laterosensory canal that extends as a continuous ossification to the level of the quadrate's articular facet is typical for characiforms (e.g., the curimatid, *Potamorhina latior*, Figure 27). The Anostomidae and Prochilodontidae, in contradistinction, have the anterior portion of the preopercular laterosensory canal enclosed by two or three discrete ossified tubes aligned along the ventral surface of the quadrate (Figures 28, 29). These separate ossifications were termed the subpreopercles by Roberts (1973:218), whereas Winterbottom (1980:37) considered them to be part of the preopercle. The homology of these ossified tubes in the two families is questionable. Even if homologous, the overall most parsimonious hypothesis of relationships that includes the two families indicates that the separate ossifications in anostomids and prochilodontids represent independently achieved adaptations to functional requirements that can only be speculated upon. At least for the Prochilodontidae, Winterbottom's terminology is preferred, because it is considered more reflective of the probable homology of the elements. The autogenous ossifications in that family occur in the region plesiomorphously oc-

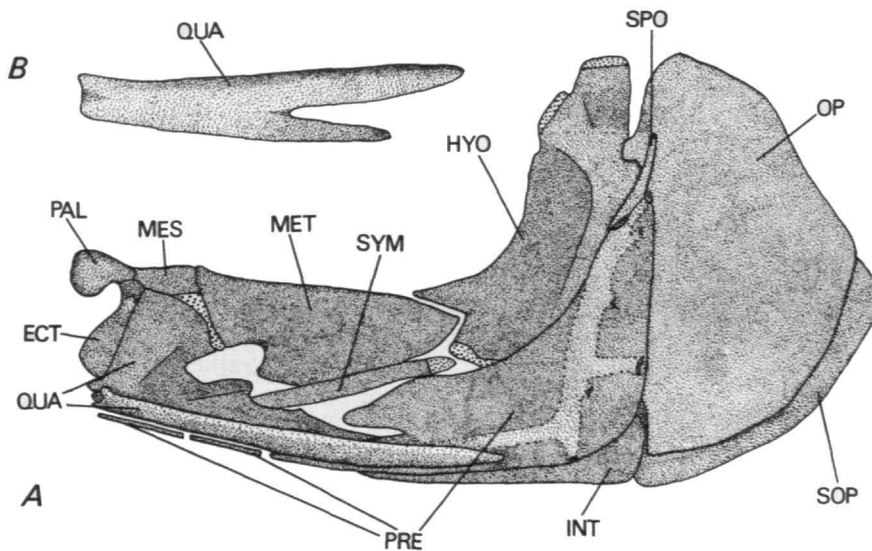


FIGURE 29.—*Leporinus fasciatus*, USNM 103847: A, suspensorium, left side, lateral view; B, quadrate, left side, ventral view.

cupied by the anterior portions of the preopercle (Figure 28). An anterior subdivision of the preopercle in prochilodontids is necessary for vertical motion of the quadrate on the preopercle. Such mobility would be impossible or greatly restricted if prochilodontids retained the primitive rigid preopercle that extends along the anteroventral surface of the quadrate. A hypothesis that the separate ossifications arose via a fragmentation of the attenuate anterior portions of the preopercle is, thus, the simplest. The alternate assumption, inherent in Robert's terminology, that the tubes are nonhomologous with portions of the preopercle, would necessitate the loss of the anteriormost section of the preopercle ventral to the quadrate followed by the development of two or three new, autogenous elements.

The quadrate-preopercle joint in anostomids is immobile. Thus, the anterior subdivision of the preopercle in that family cannot be ascribed to the same underlying functional explanation advanced for prochilodontids, more so because the phylogenetic reconstruction indicates that the modifications are homoplasious. The anostomid suspensorium (Figure 29) has undergone a pronounced anterior elongation with a consequent wide separation of the anterior terminus of the quadrate and, thereby, the lower jaw from the main body of the preopercle. Under such circumstances the maintenance of continuity between the laterosensory system of the preopercle and lower jaw necessitates a pronounced lengthening of the preopercular laterosensory canal along the ventral margin of the quadrate. If that extension took place via a progressive ossification of the anterior portion of the preopercular sensory canal, then the extremely attenuate ossified tube that results might subsequently subdivide. Alternatively, the laterosensory system might extend forward as an unossified canal, which is subsequently partially strengthened by autogenous ossifications that developed anterior to the preopercle *per se*. Data relevant to a selection between these alternative possibilities is not available at this time. The most parsimonious hypothesis of relationships for anostomids, prochilodontids, and their close relatives indicates that under

either scenario the autogenous preopercular laterosensory canal ossifications are homoplasies in prochilodontids and anostomids.

The highly modified genus *Gnathodolus* differs from other anostomids in its lack of the separate anterior preopercular ossifications (Winterbottom, 1980, fig. 41). The absence of the ossifications in that genus is most parsimoniously considered a secondary loss in light of the phylogenetic distribution of the ossifications and our present information on relationships within the Anostominae (Winterbottom, 1980).

Most anostomids have the horizontal portion of the quadrate posteriorly bifurcate, as among prochilodontids (Figures 28B, 29B). However, in anostomids the relationships of the quadrate's medial process with the preopercle differ from the prochilodontid condition, thereby, casting doubt on the homology of the modifications in the two families. The quadrate's medial process in prochilodontids runs internal to the preopercle with the longitudinal midline of the resulting quadrate notch aligned with the anteroposterior axis of the ventral portion of the preopercle. In conjunction with other previously discussed suspensorium modifications, this restructuring of the quadrate permits vertical mobility of that bone on the preopercle. In anostomids, in contrast, the distinct posterior notch in the preopercle, when present, is largely a consequence of the posterior expansion of the bone's lateral portion rather than the common posterior development of its medial and lateral processes. The midline of the notch defined by the medial and lateral processes of the anostomid quadrate's posterior region is not aligned with the longitudinal axis of the preopercle but, rather, lateral to it. Consequently, the medial quadrate process does not extend internal to the preopercle, but, rather, often inserts into a notch in that bone to form an immobile joint. In light of these differences, the equivalence of the posterior quadrate bifurcation in prochilodontids and anostomids is questionable, more so since the most parsimonious hypothesis of relationships of the involved families indicates that these are homoplasies.

A final suspensorium character of note involves

the hyomandibula in anostomids and chilodontids. In both families, that bone has a variously developed process that extends over the posterodorsal portion of the metapterygoid. The possession of such a process is evidently derived within characiforms and is not known in prochilodontids and curimatids. It is found, evidently as an independent acquisition, in some serrasalmines (*Collossoma*), parodontids (*Parodon*, *Saccodon*), hemiodontids (*Bivibranchia*), and characids (*Acestrorhynchus*).

Gregory and Conrad (1938), followed by Géry (1961), apparently misinterpreted the identity of certain elements in the anostomid suspensorium. Comparisons of the illustration of the osteology of an unspecified *Leporinus* species in Gregory and Conrad's figure 28 with Figure 29 of this study shows their metapterygoid is actually a portion of the hyomandibula. The entopterygoid (= mesopterygoid) of those authors should be more properly identified as the metapterygoid. The unlabelled ectopterygoid and palatine are illustrated so as to appear as portions of the quadrate and lateral ethmoid, respectively. Géry's more detailed illustrations of *Leporinus*' head osteology (1961, figs. 12, 14) have similar problems. The element labelled as the palatine in his drawing of *L. friderici* is actually a composite of that element and the mesopterygoid. This error results in the remaining elements in the series being sequentially misidentified. His entopterygoid (= mesopterygoid) should be identified as the metapterygoid. The element labelled by Géry as the metapterygoid is actually the anteroventral section of the hyomandibula. Géry illustrates a joint between a posterodorsal, triangular hyomandibula, and a vertically oriented metapterygoid. That line of demarcation actually represents the location of a distinct ridge along the lateral surface of the hyomandibula, rather than a point of contact between two bones. The actual hyomandibula of *Leporinus* is equivalent to the hyomandibula plus metapterygoid of Géry's illustration. As a consequence of these misinterpretations, Géry's osteological description of various portions of the suspensorium (1961:104) is misleading, particularly the comments on the relative size of

the hyomandibula in anostomids.

The synapomorphic form of the second infraorbital of prochilodontids is the only phylogenetically significant character within the circumorbital series at the family level of the four-family group. All prochilodontids examined have the ventral margin of the bone anteroventrally expanded into a distinct triangular process. The anterior border of that process, the ventral margin of the enlarged first infraorbital and the anteroventral edge of the second infraorbital delimit a triangular notch that borders the posterior margin of the large fleshy lips (Roberts, 1973:229). No similar alteration of the second infraorbital was found in the characiform outgroups examined in the present study.

Gregory and Conrad (1938:348) reported that a supraorbital is absent in the anostomid genus *Leporinus*, an erroneous observation corrected by Géry (1961:103). Géry's illustrations of the circumorbital series and the dermal ossifications anterior to the orbit (1960, fig. 2; 1961, figs. 12, 15) utilized osteological terminology inconsistent with that of previous and subsequent authors. The ossification he labels as the lachrymal is the bone that Weitzman (1962:28) termed the antorbital. No other author dealing with characiforms has identified the antorbital as the lachrymal and such a homology appears to be erroneous. The lachrymal of teleosts has traditionally been equated with the anteriormost (first) infraorbital, whereas Géry (1960, fig. 2; 1961, figs. 12, 15) labelled the anteriormost infraorbital as the jugal in his figures. The use of jugal for a subunit of the infraorbital series in ostariophysan fishes apparently follows Gregory and Conrad (1938). Those authors, however, used jugal and infraorbital 2 interchangeably, whereas Géry applied the term to the first infraorbital.

#### PECTORAL GIRDLE

The common name for chilodontids, headstanders, refers to their oblique, head-down swimming orientation (Géry, 1977b:212-213). This highly unusual swimming position and the resultant atypical forces that act on the body perhaps

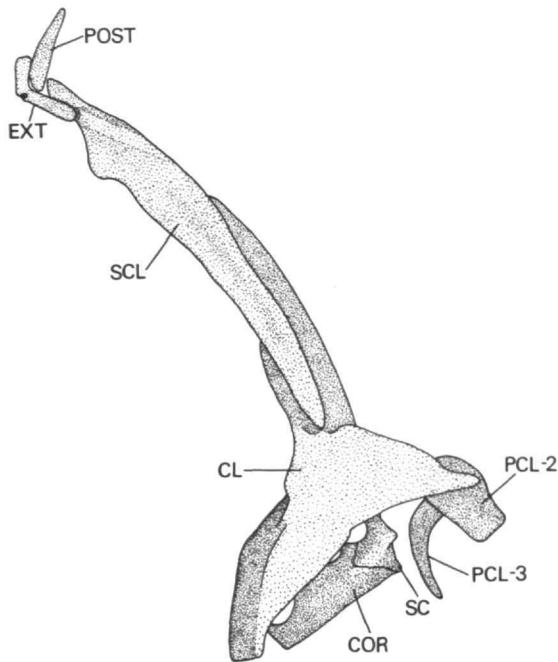


FIGURE 30.—*Caenotropus maculosus*, USNM 231545, pectoral girdle, left side, lateral view (radials and pectoral fin rays removed).

account for most of the numerous unique pectoral girdle modifications in the family. Examination of the overall form of the girdle shows that the proportions of the major elements differ markedly from those encountered in other characiforms. Unlike many characiforms, chilodontids have a cleithrum with a distinct posterior development of the lamina above the pectoral fin base (Figure 30). More notable is the ventral expansion of the supracleithrum's main shaft over the cleithrum's lateral surface. Consequently, the supracleithrum's length is well over half of the girdle's total vertical span. The increased overlap of the cleithrum on the supracleithrum increases the internal rigidity of the pectoral girdle, with the flexibility of that complex on the neurocranium reduced by alterations of the supracleithrum, posttemporal, and pterotic. With few exceptions, characiforms have the pectoral girdle attached to the neurocranium via a relatively complex posttemporal. In the typical condition the posttemporal's main body is triangular and gives rise to

two primary processes (Weitzman, 1962, fig. 19). The dorsal process of the posttemporal extends dorsomedially along the posterior edge of the parietal, to which it is tightly attached. A second smaller, strut-like process extends from the ventromedial surface of the posttemporal to contact the rear of the neurocranium. The laterosensory canal segment in the posttemporal's ventral portion communicates anteriorly with the sensory canal of the extrascapular and posteroventrally with that in the dorsal portion of the supracleithrum. The typical characiform extrascapular is triangular with a tripartite laterosensory system that contacts the canals of the pterotic anteriorly, posttemporal posteriorly and parietal dorsally.

The chilodontid posttemporal is greatly altered relative to the hypothesized plesiomorphous morphology described above. The bone is reduced ventrally, with the ventromedial posttemporal process and the laterosensory canal segment absent. The dorsal, relatively unaltered, portion of the bone is elongate, tapers dorsally and attaches firmly to the posterior margin of the parietal (Figure 31). The reduction of the posttemporal's

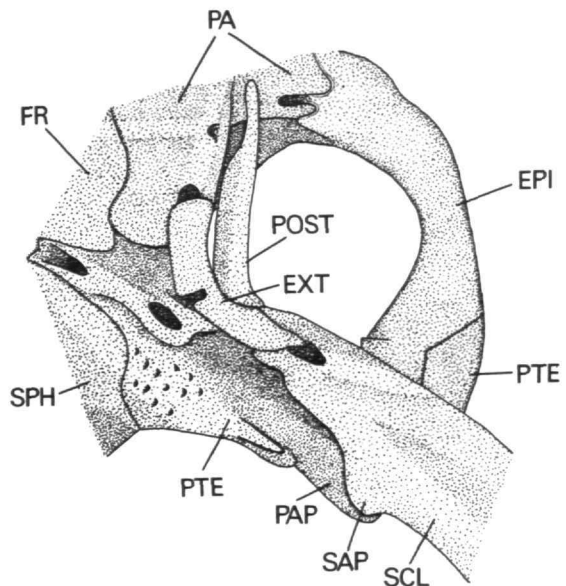


FIGURE 31.—*Caenotropus maculosus*, USNM 231545, dorsal portion of pectoral girdle and posteroventral portion of neurocranium, left side, lateral view.



laterosensory canal segment and the supracleithrum's dorsal expansion result in direct contact of the extrascapular and supracleithral laterosensory canal segments. A reduced posttemporal sensory canal typically occurs in various smaller characiforms that have an overall reduction in head ossification. In those taxa, however, this reduction results in a gap in the laterosensory canal system rather than direct communication between the canals of the supracleithrum and extrascapular as in chilodontids. The plesiomorphously present ventromedial posttemporal process is also absent in some parodontids and in various less well-ossified characiforms assigned to a number of different families. The information of this study and other data indicates that it is most parsimonious to consider the chilodontid posttemporal reduction as nonhomologous with those in the outgroups. The chilodontid extrascapular is less elaborate than that common to most characiforms. The anterior laterosensory canal is absent as a distinct process, being represented only by an anterior opening midway along the margin of the remaining ossified tube.

The marked reduction in the relative size and complexity of the chilodontid posttemporal eliminates that element as the primary junction of the pectoral girdle and neurocranium. Rather, in chilodontids the primary dorsal articulation between the pectoral girdle and the neurocranium is achieved via the insertion of the dorsal tip of the supracleithrum into a distinct pocket in the posteroventral corner of the pterotic (Figure 31). The expanded dorsal portion of the supracleithrum is overlain dorsolaterally by the reduced extrascapular and is bordered dorsally by the remaining dorsomedial portion of the posttemporal. No comparable direct pterotic-supracleithral contact has been found in the other characiforms examined, nor has a similar association of the supracleithrum with the posttemporal and extrascapular been encountered in the order.

Chilodontids also have a second area of pterotic-supracleithral articulation. The posteroventral corner of the characiform pterotic typically bears a distinct process that ranges in form from a short spur to a distinct spine that approaches,

or even contacts, the medial surface of the supracleithrum. *Chilodus* and *Caenotropus* have that pterotic process posterolaterally expanded into an obliquely aligned, flattened plate. That plate contacts the medial surface of, and corresponds in form to, an associated anterior process of the supracleithrum (Figure 31). This articulation, together with the above-described dorsal joint between the pterotic and dorsal tip of the supracleithrum, renders the pectoral girdle immobile relative to the neurocranium. Although a contact of the supracleithrum with the posteroventral process of the pterotic occurs in various characiforms, such as articulation via a distinct distally widened posteroventral pterotic process has been encountered in only one group of nonchilodontid characiforms. The African family Citharinidae has the posteroventral portion of the pterotic flared outwards into a slightly bi-pronged plate that contacts the medial surface of the supracleithrum's dorsal portion. Comparison of these functional complexes in chilodontids and citharinids reveals that the pterotic expansion in the Citharinidae differs in overall form from the distally ovoid supporting process of the Chilodontidae. The citharinid supracleithrum also lacks the well-developed anterior process that articulates with the pterotic in chilodontids. Citharinids, furthermore, do not possess the other distinctive pectoral girdle modifications of chilodontids and the Citharinidae shares uniquely derived characters with, and is evidently most closely related to, the Old World Distichodontidae (Vari, 1979:324). These factors support a hypothesis of the independent acquisition of the more ventral of the pterotic-supracleithral contacts in the Chilodontidae and Citharinidae.

Three postcleithra along the posterior margin of the pectoral girdle are typical for characiforms. The dorsalmost (postcleithrum 1) is a flattened, round ossification located at the posterior margin of the contact area of the supracleithrum and cleithrum. Postcleithrum 2 is usually a flattened, ovoid bone at the rear of the cleithrum's posterior lamina. The straight or slightly curved, rod-like postcleithrum 3 attaches to the medial surface of postcleithrum 2 and extends ventral of the latter

element. Postcleithra of this type are common to most curimatids, prochilodontids and anostomids. Chilodontids, however, have that system modified both at the familial and intrafamilial levels. In all members of that family, postcleithrum 1 is lacking (Figure 30). Although the absence of the element is considered derived, its lack is not unique to this family within the Characiformes. No postcleithra are present in the gastropolecins of the family Characidae (Weitzman, 1954:226). Postcleithrum 1 is also missing in the African hepsetid characoid *Hepsetus* (Roberts, 1969:426), the distichodontids *Nannocharax* and *Hemigrammocharax* (Vari, 1979:311) and the New World anostomid genera *Synaptolaemus* and *Sartor* (Winterbottom, 1980:46) among others. Nonetheless, the results of this study and our present understanding of phylogenetic relationships in the order indicate that the losses in those taxa are homoplasious relative to the absence of the element in chilodontids. Within the Chilodontidae, two different conditions of the third postcleithrum exist. The bone is altered into a highly curved, anteromedially shifted ossification in *Caenotropus* (Figure 30), but is totally lacking in *Chilodus*. The utility of these postcleithral adaptations in phylogenetic reconstruction is reduced by the existence of two equally parsimonious explanations for the distribution of these characters. First, the curved third postcleithrum actually represents a synapomorphy for all chilodontids, with the bone having been subsequently lost in *Chilodus*. Second, the form of the bone in *Caenotropus* and the absence of the ossification in *Chilodus* each represent synapomorphies for their respective genera independently modified from the generalized characiform type of third postcleithrum. Present data do not permit a decision as to which of these explanations is preferable.

The numerous pectoral girdle modifications in the Chilodontidae contrast with the relatively invariant forms of that system, at least at the family level, in the Curimatidae, Prochilodontidae, and Anostomidae. The single exception involves the anostomid extrascapula. The extrascapular laterosensory system of characiforms is typically tripartite with a single posterior aper-

ture that communicates with the sensory canal of the supracleithrum. The anostomid extrascapular has an additional posterodorsal sensory canal segment opening onto the posterior or posterodorsal margin of the bone. The resultant quadripartite system is not encountered in the other families under discussion. Gregory and Conrad (1938, fig. 28) mistakenly illustrate the extrascapular (their scalebone) of *Leporinus* as carrying a tripartite laterosensory canal; an error repeated by Géry (1961, figs. 12, 16) in his discussion of *Leporinus friderici*. However, all specimens of *L. friderici* and other *Leporinus* species examined have the quadripartite extrascapular laterosensory canal system herein considered typical for anostomids.

#### NEUROCRANIUM

Pronounced differences in aspects of neurocranial morphology occur in each of these families. Many, including subtle differences or continuous variation in the form or proportions of various bones, are difficult to quantify and/or polarize. The characters noted in the following discussion, consequently, tend to be discrete apomorphies, many of which were previously noted in association with changes in other body systems, with which they are functionally associated. Such previously discussed characters are only cited in passing in this section.

The mesethmoid is very broad in curimatids, with the large associated cartilagenous ethmoid block particularly distinctive. That cartilage mass fills the space between the mesethmoid dorsally and the vomer ventrally and has posteriorly directed lateral processes that contact the corresponding anterior projections of the lateral ethmoid. This cartilage mass undergoes a progressive laminar ossification of its exposed surfaces, but the major portion remains as an unossified block even in adults. Such a large cartilagenous ethmoid block has also been found only in the African Citharinidae among characiforms examined in the present study. The similarities in the ethmoid region morphology may be a reflection of their common microphagous feeding habits, but these similarities are homoplasious under our

present concepts of characiform phylogeny. These concepts indicate that the Citharinidae and Curimatidae are not each others closest relatives (see "Phylogenetic Reconstruction" and Vari, 1979).

The mesethmoid in the Chilodontidae, in contradistinction to that in curimatids, is laterally compressed and anteroventrally developed into a distinctly angled process that extends between the medial margins of the premaxillae (Figure 32). The ventral expansion of the mesethmoid results in the total separation of the premaxillae and, more interestingly, in the mesethmoid contributing to an appreciable portion of the margin of the upper jaw (see "Teeth and Jaws"). As noted on page 10, this ethmoid region morphology is evidently synapomorphic for the members of the Chilodontidae.

The Curimatidae has reduced the flexibility of the suspensorium on the neurocranium via a distinct direct articulation between the lateral ethmoid and palatine (Figure 25). The typical characiform lateral ethmoid has a discrete narrow edge along the entire lower margin of its ventral wing. In curimatids, there is instead a distinct longitudinal expansion of the ventral midsection of the wing into a cartilage-capped articular facet, which contacts a similar palatine process. As discussed in the description of the suspensorium, this is evidently a synapomorphy for all curimatids.

Associated with the overall changes of the pec-

toral girdle in the Chilodontidae are two adaptations of the pterotic, which serve to reduce the mobility of the pectoral girdle relative to the neurocranium. These were discussed at length in the section on the pectoral girdle (p. 34).

Variation exists within the Characiformes both in the number of posttemporal fossae and in the bones that border some of the apertures. The vast majority of characiforms are characterized by a dorsal and posterodorsal pair of fossae on either side of the neurocranium. Curimatids possess those apertures and an additional third small round fossa entirely within the epioccipital. This type of third posttemporal fossa also occurs in the Hemiodontidae (Roberts, 1974:416, fig. 5) and Parodontidae (Roberts, 1974:425, fig. 59). A more extensive, vertically ovate third posttemporal fossa bordered by both the epioccipital and exoccipital is found in the Old World characiform families Citharinidae and Distichodontidae (Vari, 1979, fig. 15) and the Neotropical characid tribe Cynodontini (Vari, 1979:289).

The presence of an epioccipital or epioccipital-exoccipital posttemporal fossa is apparently derived within the Ostariophysi with the epioccipital portions of each aperture presumably homologous. Comparable apertures have not been reported or discovered in characiforms outside of these groups or in other otophysans. The possession of such openings would, thus, appear to be apomorphic within the order. The available

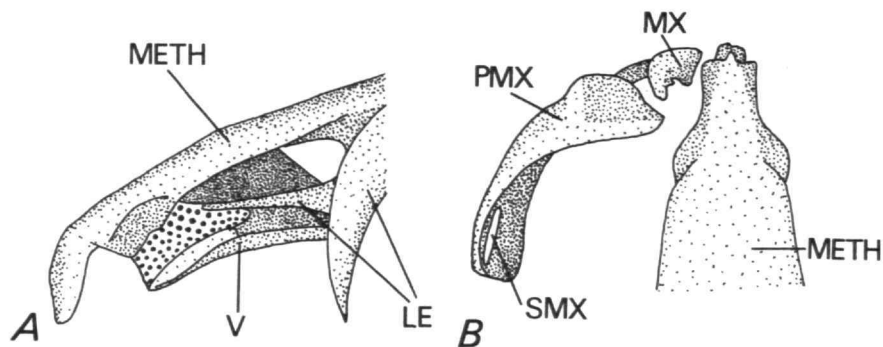


FIGURE 32.—*Caenotropus maculosus*, USNM 231545: A, anterior portion of neurocranium, left side, lateral view (large stippling represents cartilage); B, anterior portion of neurocranium and upper jaw, dorsal view.

information does not, however, permit a polarity determination on the presumed transition series between the epioccipital limited and epioccipital-exoccipital bordered forms of third posttemporal fossae.

The exact phylogenetic relationships of the two other characiform families with the curimatid form of epioccipital fossa have not been rigorously examined. Hemiodontids (sensu Roberts, 1974) have a median orbital ossification, the rhinosphenoid, unique to a subunit of the Characiformes among fishes. The possession of that element is, thus, considered a synapomorphy uniting the components of that assemblage. That character and others unite the Hemiodontidae most closely to characiforms other than curimatids, which lack the bone. The phylogenetic relationships of the Parodontidae are enigmatic. Roberts (1974:429) noted various characters common to the Parodontidae and Hemiodontidae. However, he felt that traditional concepts of a close relationship of the two families were not well corroborated. In the absence of a tested hypothesis of the relationships of parodontids to a group of noncurimatid characiforms, I can only note that the series of characters that unite curimatids with prochilodontids, anostomids, and chilodontids, which lack the opening, would indicate that the common possession of an epioccipital posttemporal fossa in curimatids and parodontids is homoplasious.

Curimatids and prochilodontids share a distinctive modification of the basic characiform bauplan of the neurocranium's posterior region. The most widespread and hypothesized plesiomorphous characiform condition of the portions of the exoccipitals proximal to the foramen magnum is illustrated in Figures 33A and 34. The exoccipitals are complex, paired elements in contact medially. Each exoccipital articulates ventrally with the median basioccipital and along its dorsal border contacts the unpaired supraoccipital. The dorsal portions of the exoccipitals meet medially along a vertical joint that extends ventrally from the articulation of the exoccipitals with the supraoccipital to the foramen magnum. Ventral to that area of midline contact, the pos-

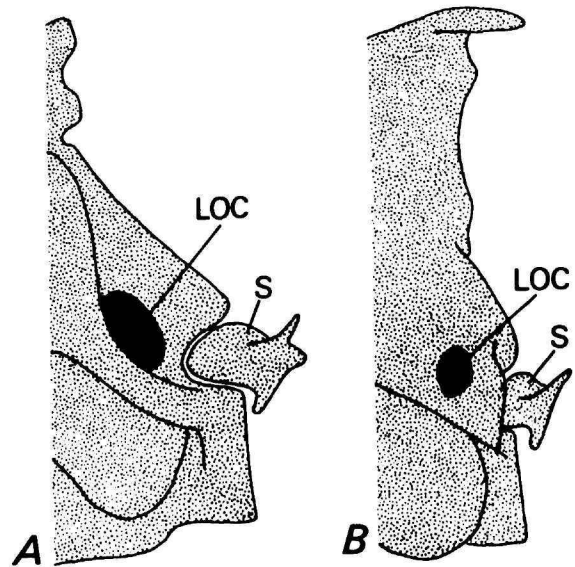


FIGURE 33.—Scaphium and rear of neurocranium, left side, lateral view: A, *Leporinus reinhardti*, AMNH 40104SD; B, *Psectrogaster amazonica*, AMNH 40088SD. (Scale = 5.0 mm.)

teromedial margins of the exoccipitals diverge laterally to form a median arch. The resultant opening encompasses the lateral borders of the foramen magnum dorsally, and the cavum sinus imparis ventrally. A horizontal sheet of bone extends from the medial surface of the main body of each exoccipital to meet its counterpart at the midline. The shelf formed by those processes serves both as the floor of the foramen magnum and roof of the cavum sinus imparis. In lateral view (Figure 33A), the posterior margin of the exoccipital proximal to the foramen magnum is distinctly concave. Viewed from the rear (Figure 34) the region of concavity is seen as a bony pillar bounded by the lateral occipital foramen and foramen magnum, with an indentation, the fossa for the scaphium, present on its posterior surface. The concave medial lip of this scaphial fossa corresponds in shape to, and closely approximates, the anterior margin of the first Weberian ossicle, the scaphium, to which it is ligamentously connected. In the majority of characiforms out-

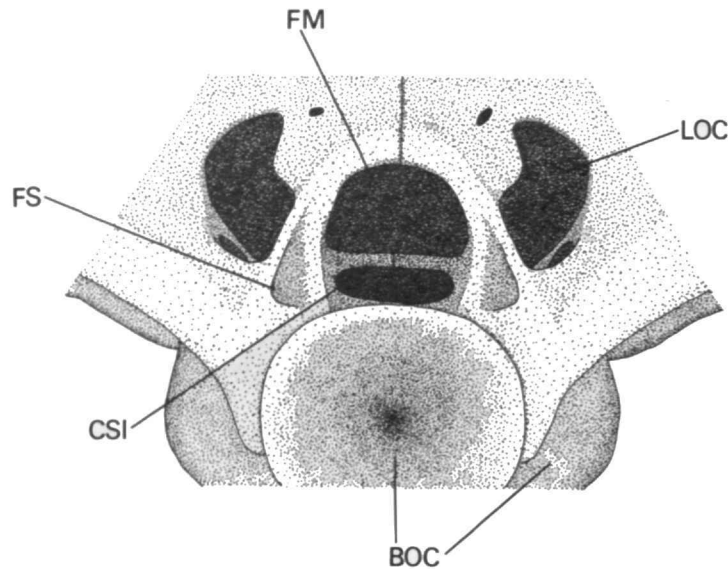


FIGURE 34.—*Leporinus reinhardti*, AMNH 40104SD, region of foramen magnum, posterior view.

side of curimatids and prochilodontids, the fossa ranges from a negligible depression in some anostomids (Figure 34) to a distinct cul-de-sac in characids such as *Brycon* (Weitzman, 1962, fig. 5). A foramen, the lateral occipital fenestra, is typically found along the midlateral surface of the exoccipital. That aperture's degree of development differs within the order, ranging from a barely apparent foramen to a large opening occupying most of the surface of the exoccipital lateral to the foramen magnum. The lateral occipital fenestra typically has a nearly vertical orientation and serves, at least in part, as a passage for nerves.

Curimatids and prochilodontids share a distinctive restructuring of the portion of the exoccipital bounded by the lateral occipital foramen and the foramen magnum. In both families the plesiomorphous cul-de-sac fossa for the scaphium is greatly expanded laterally and anteriorly (Figure 35). As a consequence the slightly or moderately developed scaphial fossa common to most characiforms is altered in curimatids and prochilodontids into a large foramen that is continuous anterolaterally with the lateral occipital for-

amen and communicates anteriorly with the neurocranium's interior. This expanded fossa for the scaphium subdivides the primitively single vertical pillar bounded by the foramen magnum and lateral occipital foramen into two parts (Figure 35). The medial portion that borders the foramen magnum and cavum sinus imparis is deeply indented to accommodate the anterior margin of the scaphium to which it is ligamentously attached. A marked outwards shift of the primitively lateral edge of the fossa results from the expansion of that aperture. Thus, the associated portion of the exoccipital's lateral surface is now more obliquely aligned than in the hypothesized primitive condition. With this change in inclination the opening of the lateral occipital fossa faces more posterolaterally in curimatids and prochilodontids than in other characiforms.

The rear margin of the exoccipital lateral to the enlarged fossa for the scaphium is also posteriorly expanded. This expansion results in a single inclusive opening leading to the foramen magnum, cavum sinus imparis, and the paired scaphial fossae. The foramen magnum and sinus cavum imparis apertures are consequently in-

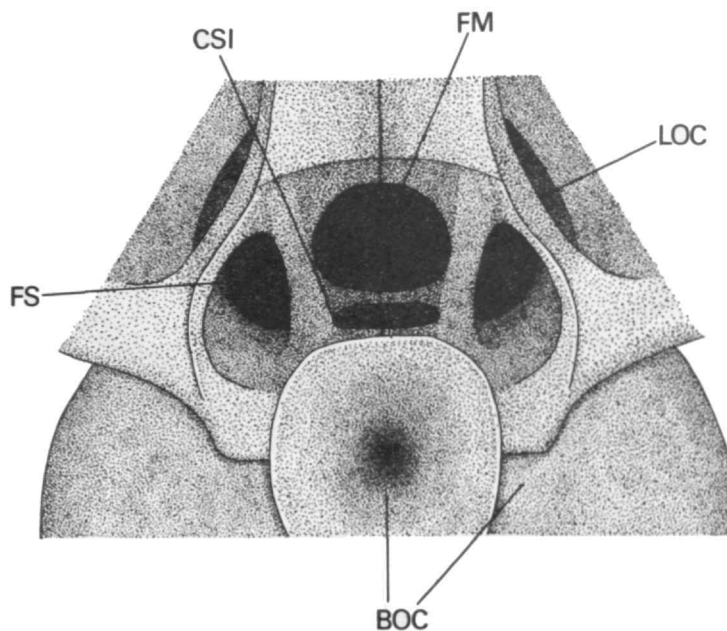


FIGURE 35.—*Psectrogaster amazonica*, AMNH 40088SD, region of foramen magnum, posterior view.

cluded in the neurocranium rather than located along its posterior margin as in the primitive condition. The posterior extension of the lateral margin of the exoccipital also results in the posterior portion of that element overlapping the scaphium's anterior section to the level of the attachment point of the interosseus ligament (Figure 33b).

Examination of a wide variety of other characiforms and Ostariophysans has revealed only a single group, the Gasteropelecinae, with comparable exoccipital modifications (Weitzman, 1954:218, figs. 5, 10). The gasteropelecine exoccipital, as that in curimatids and prochilodontids, has the deep foramen form of fossa for the scaphium. This results in the inclusion of the foramen magnum, cavum sinus imparis, and paired scaphial fossae in a large common opening and the anterior overlap of the scaphium by the exoccipital's margin. The only significant difference between the gasteropelecine exoccipital and that common to curimatids and prochilodontids occurs in the position of the lateral occipital fora-

men. In gasteropelecins the foramen's lateral opening is shifted ventrally to a deep fossa barely posterodorsal to the lagenar capsule. With this repositioning, the foramen's opening is now directed ventrolaterally, whereas a lateral orientation is common to the majority of characiforms, and a slightly dorsolateral alignment is shared by curimatids and prochilodontids. The ventral position and ventrolateral orientation of the foramen in gasteropelecins, contrary to the more dorsal location and slightly dorsolateral alignment of the aperture in prochilodontids and curimatids, is not, in itself, evidence of the nonhomology of the other shared exoccipital modifications. The variation in lateral occipital foramen position might rather represent different apomorphic adaptations of a shared derived ancestral condition common to curimatids, prochilodontids, and gasteropelecins.

A hypothesis of the homoplasy of the exoccipital alterations must, therefore, depend on a phylogenetic reconstruction of greater generality within characiforms. The results of this study

indicate that the phylogenetic relationships of curimatids and prochilodontids lie with characiforms other than gasteropelecins (see "Phylogenetic Reconstruction"). The question of the possible relatives of gasteropelecines within characiforms has not been critically analyzed, using more recently formalized systematic procedures. Nonetheless, Weitzman's conclusion (1954:231) that "the Gasteropelecinae probably arose from some generalized characid somewhat like *Ashtyanax*, *Brycon*, and *Bryconamericus*" is consistent with our present knowledge of character polarities and phylogenetic relationships within the Characiformes. Although we are presently unable to rigorously test a hypothesis of the probable homoplasy of the exoccipital modifications of gasteropelecins on the one hand and those in the assemblage consisting of curimatids and prochilodontids on the other, the available data, nonetheless, indicates that these seemingly equivalent characters represent convergencies.

A final neurocranial character of note is the size of the lagenar capsule of curimatids. In the Curimatidae, the capsule is significantly expanded into a large bulbous chamber. The apomorphic enlargement is notable both relative to the condition in the other three families under consideration and the various characiform outgroups examined.

#### VERTEBRAL COLUMN AND RIBS

A variety of derived characters that involve the anteriormost pleural ribs and the associated vertebrae occur in anostomids and chilodontids. One of the more distinctive characters common to these families are the two or more discrete, well-developed intercostal ligaments that join the midsections of three or more of the anteriormost full pleural ribs. These intercostal ligaments presumably are thickened sections of the broad connective tissue sheet that typically joins the medial margins of the pleural ribs. The intercostal ligaments in chilodontids are thicker than those in anostomids and span a maximum of three ribs. The ventral ligament in chilodontids arises from the posterior margin of the first full pleural rib,

extends obliquely posterodorsally to attach to the medial surface of the second rib, and terminates posteriorly on the anterior border of the third rib (Figure 36). A second, shorter ligament, dorsal and parallel to the first, extends between the first and second ribs. Anostomids have a greater number of ribs incorporated into the system, although the individual intercostal ligaments are not as developed as in chilodontids. The ventral ligament in anostomids commences on the posterior margin of the first full pleural rib, attaches to the medial margins of the second and third ribs, and terminates posterodorsally on the anterior border of the fourth rib. A second, more dorsal, ligament extends between the first and third ribs, with an attachment to the inner surface of the second rib. The described pattern is the simplest within the family, with the number of ribs and intercostal ligaments in the system further increased in some anostomids. The ligaments' exact function is un-

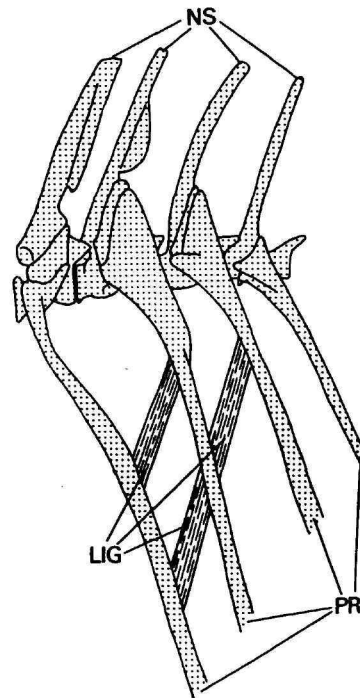


FIGURE 36.—*Chilodus punctatus*, USNM 231542, fifth to eighth vertebrae, dorsal portions of anteriormost full pleural ribs and intercostal ligaments, left side, lateral view.

certain, but the interconnected anterior pleural rib complex in these fishes may be associated with their oblique, head-down swimming position.

The oblique body orientation during locomotion is most pronounced in the Chilodontidae (Géry, 1977b:212–213), which have the thickest intercostal ligaments. The first three full pleural ribs spanned by these heavy bands in chilodontids have their proximal portions and the parapophyses, neural spines, and arches of the associated vertebrae extensively restructured. Among characiforms the typical moderately developed parapophyses on the first three full pleural ribs insert into circular or ovoid articular fossae limited to the respective centrum's lateral surface (Weitzman, 1962, fig. 12). However, the chilodontids *Caenotropus* and *Chilodus*, have the proximal portions of the first three full pleural ribs expanded dorsally, which results in the proximal portions of the ribs having a triangular form with maximum vertical development in the region adjoining the parapophyses (Figure 37). The parapophyses are also expanded vertically relative to the ossification in other characiforms. The dorsally

elongate medial surface of the parapophyses articulates with a vertically elongate fossa. That articular surface incorporates ventrally the pleiomorphous small fossa on the lateral face of the centrum and a vertically elongate flange on the lateral surface of the neural arch and spine (Figure 37). Such lateral elaborations of the neural arch and spine are unknown elsewhere in the order. This degree of dorsal development of the components of this complex is greatest on the second full pleural rib and associated portions of the sixth vertebrae. This development is also apparent, though not as pronounced, on the first and third full pleural ribs. The consolidation that results from these adaptations eliminates the motion of the dorsal portions of the ribs relative to the vertebral column, particularly given the more distal interconnections of these ribs via the aforementioned intercostal ligaments.

#### MYOLOGY

Considerable variation exists in the morphology of the jaws, suspensorium, gill arches, and the parts of the neurocranium associated with those systems among curimatids, prochilodontids, anostomids, and chilodontids. Congruent with the osteological changes are a series of adaptations of the associated musculature.

Two myological apomorphies have already been described in the discussions of the gill arches and epibranchial organs. The first is the distinctive vertical muscle band that extends along the anterior and posterior surfaces of the chilodontid epibranchial organ's dorsal portions (see "Epibranchial Organs"). The other is the greatly thickened obliques dorsalis associated with the highly modified fourth gill arch in the Anostomidae and Chilodontidae (see "Gill Arches").

The form of the adductor mandibulae is hypothesized to be synapomorphic for the four-family unit. In his discussion of the cheek musculature in *Leporinus*, Alexander (1964:183–184) noted the presence of a discrete medial portion of the adductor mandibulae, which he suggested was the A<sub>3</sub> section of that muscle. That homology is reasonable within the context of our present

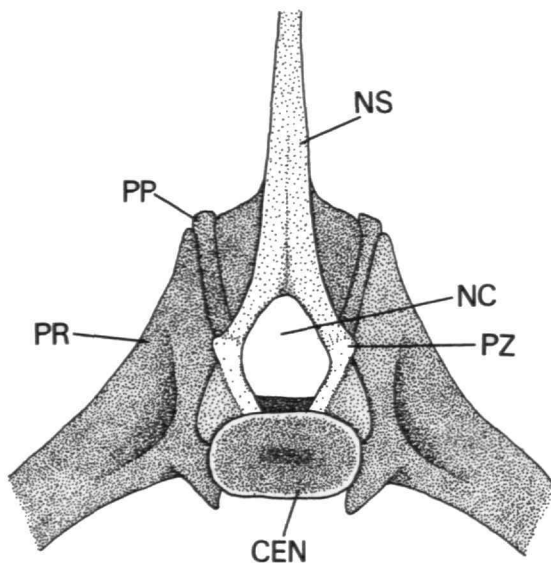


FIGURE 37.—*Chilodus punctatus*, USNM 231542, sixth vertebra, parapophyses, and dorsal portion of pleural ribs, anterior view.



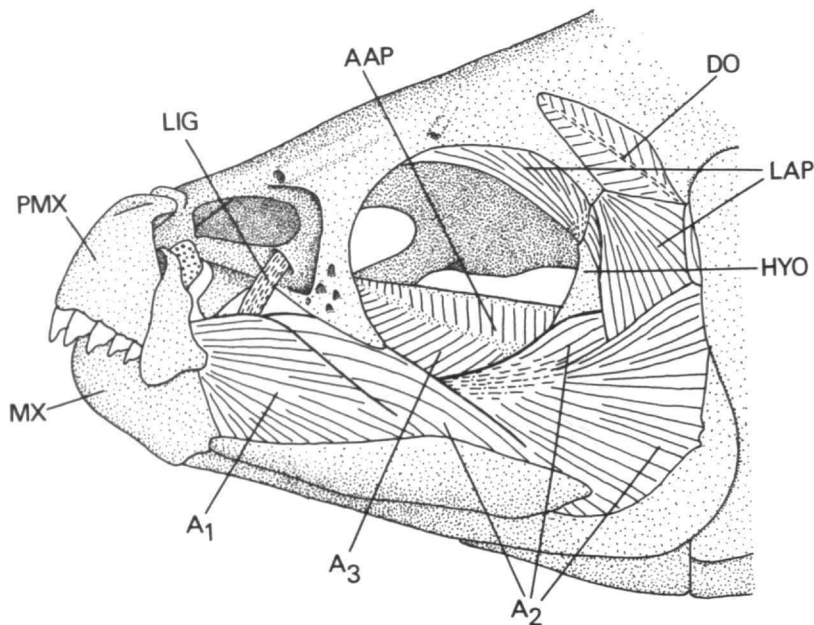


FIGURE 38.—*Leporinus striatus*, USNM 231948, cheek and suspensorium musculature, left side, lateral view.

understanding of characiform myology. A distinct  $A_3$  portion of the adductor mandibulae that arises from the lateral surface of at least the mesopterygoid and metapterygoid is common to curimatids, chilodontids, prochilodontids, and anostomids, with further pronounced apomorphic changes unique to each of the latter two families (Figures 38, 39). In its simplest condition, as in curimatids and chilodontids, the  $A_3$  is formed by a series of anterolaterally slanting fibers that have an origin on the dorsolateral surface of the mesopterygoid and metapterygoid. These muscle slips attach laterally to the tendinous band located along the medial surface of the  $A_2$  portion of the adductor mandibulae. No comparable form of  $A_3$  has been encountered in the broad, but by no means exhaustive, outgroup comparisons carried out among other characiform taxa, nor has it been reported in the literature. The  $A_3$  reported in citharinids and distichodontids (Vari, 1979:316) differs in several features. That muscle arises from the anteromedial surface of the hyomandibula and extends forward

as a discrete muscle band margined medially by a tendinous sheet, which coalesces anteriorly with the tendon of  $A_2$ . A comparable situation exists in serrasalmins. Thus, the  $A_3$  of these taxa differs in origin and mode of insertion relative to the condition of the  $A_3$  form in the Curimatidae, Prochilodontidae, Anostomidae, and Chilodontidae. Consequently the characteristic morphology of the  $A_3$  section of the adductor mandibulae is hypothesized to be a synapomorphy for the latter four-family clade.

Two sets of apomorphic modifications of the cheek musculature are characteristic for the species of anostomids on one hand and those of prochilodontids on the other. One character in the Anostomidae is particularly noteworthy. The anostomids available for myological study (*Abramites*, *Anostomus*, *Leporellus*, *Leporinus*, *Rhytiodus*, and *Schizodon*) have a triangular muscle in the posterodorsal portion of the orbital chamber (Figure 38). The V-shaped ventral portion of the muscle is capped by an aponeurotic sheet that attaches onto a discrete process on the anterodor-

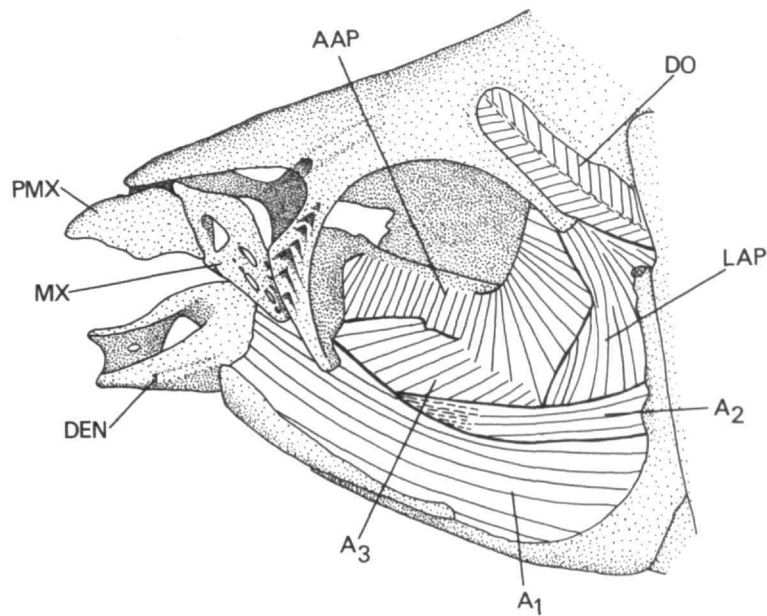


FIGURE 39.—*Prochilodus rubrotaeniatus*, USNM 225419, cheek and suspensorium musculature, left side, lateral view.

sal margin of the hyomandibula. The muscle fans out dorsally with an origin on the anteroventral face of the sphenotic and orbital surface of the frontal. The phylogenetic derivation of the muscle is uncertain, but the levator arcus palatini is the most likely source. That homology hypothesis is advanced primarily on the evidently common function of the two muscles and their general proximity. Furthermore, in some characiforms the medial portion of the levator arcus palatini overlaps the anterior margin of the hyomandibula; the medial portion also has a limited medial origin along the anteroventral face of the sphenotic spine comparable to, though not as extensive as, that of the discrete triangular muscle in anostomids. Outgroup comparisons have failed to reveal another characiform group with a similar discrete muscle.

The adductor mandibulae of anostomids is unusually altered. The  $A_1$  section of the muscle is subdivided into two portions. The first section is located along the anteroventral portion of the cheek and extends anterodorsally to attach di-

rectly to the maxilla (Figure 38). A second section of the  $A_1$ , medial to the above, arises from the entire ventral surface of the trough formed by the lateral shelf of the quadrate and preopercle. Commencing posteriorly at the terminus of the quadrate, the muscle extends anteriorly with a tendinous band along its dorsomedial margin. That connective tissue sheet progressively thickens anteriorly to form a distinct tendon, which attaches to the maxilla. The  $A_2$  portion of the adductor mandibulae is significantly more highly developed transversely in anostomids (Figure 38) than in chilodontids, curimatids, and prochilodontids (Figure 39). In those families, the posterior portion of the  $A_2$  section of the adductor mandibulae lies lateral to the levator arcus palatini with an origin solely from the angle of the preopercle. Such a form of the muscle is also common to numerous generalized characiforms and evidently primitive in the order. In the Anostomidae, by contrast, the posterior portion of  $A_2$  has an additional medial section that extends internally to the ventral portion of the levator arcus palatini

and has an apomorphous partial origin from a distinctly concave region of the anteroventral portion of the hyomandibula.

The junction between the posteriorly separated lateral and medial sections of  $A_2$  in anostomids is demarcated by a tendinous band, which progressively thickens anteriorly to form a distinct tendon that extends forward to an insertion on the lower jaw. A considerable portion of the median margin of that tendon serves as the insertion site for the  $A_3$  portion of the adductor mandibulae. That muscle section is greatly developed relative to the condition in curimatids, prochilodontids, and chilodontids, with this expansion particularly pronounced in the region of the ventral wing of the lateral ethmoid (Figure 38). This dorsally bulging muscle section attaches to the medial and dorsal surfaces of the ligament and joins anteriorly with the medial surface of the dorsally expanded anterior portion of  $A_2$ . The dorsal contact between these two muscle sections results in the common tendon on the  $A_2$  and  $A_3$  running internal to the muscle masses that attach to the lower jaw, rather than along their dorsal margin. Such a morphology of the musculature is considered derived in light of the absence of comparable adaptations in outgroups examined in the present study. The  $A_w$  portion of the adductor mandibulae, present in most characiforms, was not found as a separate muscle in anostomids; an apomorphous absence previously noted by Alexander (1964:183).

Not unexpectedly, the highly unusual suction mouth of prochilodontids is reflected in the myology of the cheek region (Figure 39). The most distinctive character of the prochilodontid adductor mandibulae is the great expansion posteriorly of the muscle's  $A_1$  section. As a consequence the  $A_1$  arises from across the entire horizontal arm of the quadrate and preopercle with a partial origin on the ventral portion of its vertical arm. Anteriorly the muscle has a broad direct insertion on the angulo-articular's posterior margin and an insertion on the maxilla via the primordial ligament. The posterior expansion of the  $A_1$  has excluded the  $A_2$  from most of its plesiomorphous

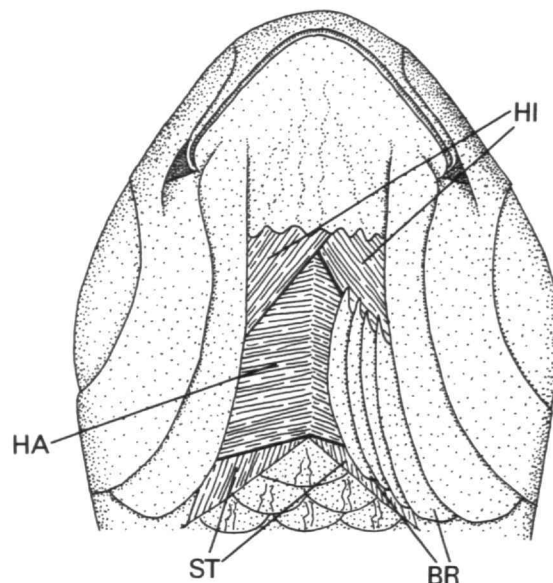


FIGURE 40.—*Prochilodus rubrotaeniatus*, USNM 225419, musculature of the ventral surface of the head, ventral view (branchiostegal rays of right side removed).

area of origin along the horizontal arm of the preopercle and ventral section of the vertical limb of that element. The  $A_2$  is consequently reduced to a relatively small, horizontally aligned band with a limited origin on the vertical arm of the preopercle in the region ventral to the insertion of the levator arcus palatini. The muscle section becomes increasingly attenuate anteriorly, giving rise to a tendinous band. The relatively large  $A_3$  attaches to the medial margin of that tendon, which then passes forward to the lower jaw. This reversal of the usual proportions of the  $A_1$  and  $A_2$  sections of the adductor mandibulae is distinctive for prochilodontids among characiforms examined.

A myological synapomorphy for the four-family clade occurs in the musculature of the ventral surface of the head. Characiforms typically have a hyohyoidei abductores with a relatively broad insertion on the dorsal surface of the branchiostegal rays. The anterior portion of the muscle progressively tapers anteriorly, with a discrete origin from the anteroventral margin of the uro-

hyal and the anteromedial surface of the hyoid arch. The posteroventral portion of the urohyal is covered by the sternohyoideus, which is readily visible in ventral view and only partially overlapped, primarily anteriorly, by the hyohyoidei adductores. In the Curimatidae, Prochilodontidae, Anostomidae, and Chilodontidae, in contrast, the hyohyoidei abductores has a broad insertion across the entire ventral surface and lateral margins of the ventrolateral wings of the urohyal, contrary to the narrow attachment to the anteriormost portion of the bone found in other characiforms (Figure 40). This broad attachment results in both the near total ventral overlap of the sternohyoideus by the hyohyoidei abductores and drastic restriction of the aperture of the gill slits. A reduction in the gill slit aperture also occurs in parodontids and some distichodontids and characids. In none of the examined outgroups is the constriction of the gill openings arrived at in a manner comparable to that in these four families. The mode in which the constriction is achieved in the Curimatidae, Prochilodontidae, Anostomidae, and Chilodontidae is consequently considered a shared derived character for the assemblage.

### Phylogenetic Reconstruction

Synapomorphies within the osteological and myological systems described in the previous section provide information relevant to a hypothesis of familial and suprafamilial relationships among the Curimatidae, Prochilodontidae, Anostomidae, and Chilodontidae. These same systems also demonstrate synapomorphies for the members of each family. The following discussion first details the synapomorphies for the four-family unit, followed by those derived characters that distinguish clades of decreasing universality within that assemblage. Subsequent to the reconstruction of the most parsimonious hypothesis of phylogenetic relationships among these families, there is a discussion of those derived characters that have a phylogenetic distribution incongruent with the arrived at hypothesis of relationships. The discussion deals both with homoplasies internal to the

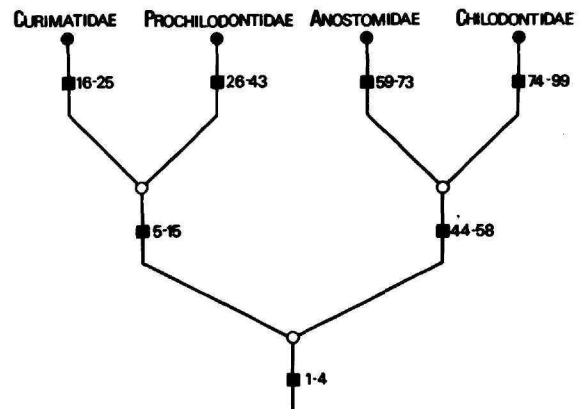


FIGURE 41.—Cladogram of the most parsimonious hypothesis of relationships of the families Curimatidae, Prochilodontidae, Anostomidae, and Chilodontidae (numbered synapomorphies correspond to those of the text).

four-family assemblage and those that involve a subunit of that lineage and a characiform outgroup. In conjunction with the phylogenetic reconstruction, that discussion provides the basis for the evaluation of previous classificatory schemes as reflectors of the phylogenetic history of the four-family assemblage and its subunits.

Figure 41 presents the most parsimonious phylogenetic hypothesis that incorporates the previously discussed synapomorphies. The apomorphic characters defining the various suprafamilial assemblages and families are numbered sequentially within clades. That procedure simplifies the visualization of character distribution and familial relationships. The numbering of the characters in the following text corresponds to the numbered synapomorphies of the cladogram in Figure 41.

### THE FOUR-FAMILY ASSEMBLAGE

The hypothesized monophyly of the assemblage formed by the families Curimatidae, Prochilodontidae, Anostomidae, and Chilodontidae is supported by the following synapomorphies for the four-family unit.

1. The elimination of the direct contact between

the fourth and fifth upper pharyngeal tooth plates.

2. The absence of dentition of the fourth upper pharyngeal tooth plate.
3. The  $A_3$  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  $A_2$ .
4. The longitudinally expanded attachment of the hyohyoidei abductores on the urohyal.

Although this hypothesis of relationships is the least robust in the phylogeny when evaluated in terms of the number of synapomorphies, it is not challenged by any equally parsimonious alternative hypothesis derivable from the characters examined. The convergencies shared by the various subunits of this assemblage with diverse characiform outgroups typically involve a single family and an outgroup rather than a monophyletic two family unit and the outgroup. Thus, hypotheses of the homoplasious nature of those characters are supported both by the synapomorphies for the four-taxon unit and the shared derived characters that unite each pair of family level sister groups. The homoplasious nature of the occurrence of such characters in and outside of the four-taxon unit under consideration is also indicated by the available data on the phylogenetic placement of the characiform outgroups that share the convergent characters. A supramaxilla, for example, is evidently limited to the Chilodontidae and the characid *Chalceus* among characiforms and is considered an independently acquired apomorphy in each of the two lineages. That hypothesis is in agreement with a parsimony evaluation, based both on the synapomorphies for the four-family unit and the more numerous shared derived characters that unite chilodontids with anostomids that lack a supramaxilla. Additional support for a hypothesis of the homoplasious distribution of the ossification comes from the various shared derived characters (e.g., common possession of a rhinosphenoid) that join *Chalceus* to the Characidae, in which a supramaxilla otherwise is absent. Considering the presence of a supramaxilla in *Chalceus* and the Chilodon-

tidae as a convergence is, thus, the simplest explanation. Comparable parsimony arguments apply to other characters homoplasiously present within the four-family assemblage and in one or more characiform outgroups. The overall distribution of such homoplasious characters does not form any other pattern consistent with an alternate concept of relationships as, or more parsimonious than, that advanced herein.

#### CURIMATIDAE AND PROCHILODONTIDAE CLADE

The less inclusive familial and suprafamilial clades among the Curimatidae, Prochilodontidae, Anostomidae, and Chilodontidae are defined by numerous advanced characters. Synapomorphies of the Curimatidae and Prochilodontidae primarily are associated with the food gathering and manipulating systems, with a lesser number being exoccipital modifications. In summary these shared derived characters are as follows.

5. The reorientation of the dorsal process of the fourth epibranchial anteriorly with its consequent extension over the dorsal surface of the fourth infrapharyngobranchial.
6. 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.
7. The large sac-like, muscular epibranchial organ that extends dorsal to the medial elements of the dorsal portion of the gill arches.
8. The conversion of the plesiomorphously flat fourth upper pharyngeal tooth plate into a curved ossification wrapped around the fourth infrapharyngobranchial.
9. The reduction or loss of dentition on the fifth upper pharyngeal tooth plate.
10. The reduction or loss of an ossified first basibranchial.
11. The absence of dentition on the fifth ceratobranchial.
12. The anteromedially directed process on the fourth ceratobranchial's ventral surface.
13. The distinct, posteroventrally aligned flange

on the lateral surface of the opercle or a further derived condition of that process.

14. The increase in the depth and width of the fossa for the scaphium that results in interconnections of the fossa with the lateral occipital foramen laterally and the interior of the cranium anteriorly.
15. The posterior development of the lateral margin 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 and a cover laterally for the anterolateral surface of the scaphium.

The phylogenetic hypothesis based on the above characters (i.e., the close relationships of the Curimatidae and Prochilodontidae) is in agreement, in whole or in part, with some previous classificatory schemes, but notably different from those of Boulenger (1904) and Roberts (1973) (see "Comparisons with Previous Classifications"). Examination of the characters that traditionally distinguish these families shows that they are largely external synapomorphies for the members of the Prochilodontidae, particularly those in mouth form, rather than any discrete external features of curimatids. Indeed, only the first listed shared derived character for the members of the latter family (see below), the toothless jaws, is apparent in external examination. Two subunits of the assemblage characterized by characters 5 to 15 are, in turn, definable by a series of synapomorphies unique to the members of each family.

#### FAMILY CURIMATIDAE

The Curimatidae is the least derived taxon among the four families under consideration in terms of the overall number of synapomorphies found during the present study. The shared derived characters congruent with the hypothesis that the Curimatidae forms a monophyletic lineage are the following.

16. The lack of dentary and premaxillary dentition.
17. The third posttemporal fossa bordered solely by the epioccipital.
18. The anteroventral process on the third hypobranchial that extends parallel to the ventral aorta.
19. The absence of an ossified first basibranchial.
20. The posteroventral expansion of the fifth upper pharyngeal tooth plate into a curved, convoluted process.
21. The secondary posterodorsal, cartilage-capped process on the palatine.
22. The cartilage-capped articular process along the ventral edge of the lateral ethmoid's ventral wing.
23. The horizontal shelf on medial surface of the metapterygoid.
24. The large cartilagenous ethmoid block and widened mesethmoid.
25. The enlarged lagenar capsule.

The absence of dentary and premaxillary dentition is the only externally apparent discrete synapomorphy for the members of the Curimatidae. Most members of the family, nonetheless, share a distinctive bauplan that permits their identification at the family level without the necessity for examination of the jaws. Some curimatids, however, differ dramatically from the typical curimatid body plan and are not readily recognized as members of the family. *Curimata ocellata* is distinctly fusiform and can be rather easily confused with some hemiodontids, which it closely parallels in body form and pigmentation pattern (Géry, 1977b, fig. 3). Alternatively, some curimatid species are extremely deep-bodied with large individuals of *Curimata abramoides* (in which the body depth exceeds 50% of standard length) representing the extreme in that direction (Kner, 1859, pl. 2).

The intrafamilial taxonomy of the Curimatidae is highly confused, with many of the nominal genera consisting of evidently unnatural groupings of species. The number of recognizable forms among the described species is uncertain. Studies to date (e.g., Vari, 1982b) have shown that about twenty of the ten dozen presently recognized species are invalid, but also that numerous previously unrecognized distinct species exist.

The taxonomic limits of the Curimatidae of this study differ from those utilized by the vast majority of prior researchers. Traditionally, curimatids and *Anodus* have been associated on the basis of their edentulous jaws. Some authors originally described various curimatid species in *Anodus* (e.g., *Anodus latior* Spix, in Spix and Agassiz, 1829) or used *Anodus* as a genus in curimatids (e.g., Eigenmann and Allen, 1942:300). Other researchers (e.g., Eigenmann and Eigenmann, 1889; Fernandez-Yepez, 1948) have reserved *Anodus* for a limited number of fusiform species known from the Orinoco and Amazon river basins. Those authors, nonetheless, either associated the genus in some unspecified manner with curimatids (Eigenmann and Eigenmann, 1889) or explicitly placed it in the Curimatidae, as the subfamily that formed the sister lineage to curimatids (*sensu stricto*) (Fernandez-Yepez, 1948:19). However, the phylogenetic affiliations of *Anodus* appear to lie with the Hemiodontidae rather than the Curimatidae (*sensu stricto*), a hypothesis first advanced by Roberts (1974) and confirmed by this study. That larger assemblage, in turn, shows various synapomorphies with some, but not all characids, to which it is apparently more closely related.

#### FAMILY PROCHILODONTIDAE

The family Prochilodontidae is a very distinctive assemblage having the following numerous shared derived characters.

26. The increased number of functional and replacement tooth rows and teeth per row.
27. The highly developed fleshy lips that form a suctorial oral disk.
28. The bulbous form of the premaxilla.
29. The bulbous form of the maxilla, the numerous maxillary fenestrae, and the posteromedial bony maxillary process that serves for the attachment of the maxillo-mandibular ligament.
30. The foreshortened dentary and the expanded, laterally rotated dentary replacement tooth trench with a large medial fenestra.
31. The reduction in the overall relative size of the retroarticular and its shift onto the medial surface of the angulo-articular.
32. The transverse compression of the fifth upper pharyngeal tooth plate and the mobility of that element with respect to the fourth epibranchial.
33. The transverse expansion of the basihyal's anterior portion.
34. The ventrally notched interhyal and the sesamoid ossification in the ligament that joins the interhyal to the posterior ceratohyal.
35. The transverse broadening of the branchiostegal rays.
36. The transverse widening of the urohyal's ventral wings.
37. The ontogenetic expansion of the opercular flange into a broad, flat, thickened region on the opercle's lateral surface.
38. The tripartite ectopterygoid that is mobile relative to the quadrate and preopercle.
39. The posteriorly notched quadrate that is vertically mobile on the preopercle and the lateral shelf on the quadrate.
40. The subdivision of the anterior portion of the preopercular laterosensory canal into two or more ossified tubes.
41. The form of the second infraorbital.
42. The posterior extension of the A<sub>1</sub> portion of the adductor mandibulae.
43. The reduction of the A<sub>2</sub> portion of the adductor mandibulae.

Prochilodontids are most readily recognizable externally by their enlarged fleshy lips, which evert into a suctorial oral disk. That mouth form is unique to the family among characiforms and the listed synapomorphies for the members of the family are all associated with oral apparatus modifications. Three genera (*Ichthyoelphas*, *Prochilodus*, and *Semaprochilodus*) with some 30 to 40 nominal species, presently are recognized, although an understanding of the actual number of valid species must await a thorough revision of the family. Many of the species are economically important and undertake large-scale, long-distance, spawning-associated migrations. Roberts (1973) has described the osteological variation in the Prochil-

odontidae and provided a partial synopsis of the available life history information for the family.

#### ANOSTOMIDAE AND CHILODONTIDAE CLADE

The Anostomidae and Chilodontidae have been the subject of divergent opinions concerning their interrelationships and the appropriate ways to reflect those concepts taxonomically. Some of the adaptations common to the two families are quite unusual, particularly the various restructurings of the branchial apparatus. Those gill arch modifications and the synapomorphies in other body systems are as follows.

44. The longitudinal foreshortening of the mandible.
45. The pronounced enlargement of the upper and lower pharyngeal dentition.
46. The presence of two or more cusps on all pharyngeal teeth.
47. The shift in the alignment of the fourth upper pharyngeal tooth plate that results in its contact with the fourth epibranchial rather than the fifth upper pharyngeal tooth plate.
48. The vertical thickening of the fifth upper pharyngeal tooth plate.
49. The transverse expansion of the posterior region of the third infrapharyngobranchial.
50. The thickening and posterodorsal reorientation of the dorsal process of the fourth epibranchial.
51. The vertical expansion of the anterior process of the fourth epibranchial.
52. The highly developed obliquus dorsalis associated with the fourth infrapharyngobranchial.
53. The longitudinal foreshortening of the hyoid arch.
54. The oblique angle of the articulation between the anterior and posterior ceratohyals.
55. The distinct cord-like ligament that joins the lateral surface of the ectopterygoid and ventral wing of the lateral ethmoid.
56. The prominent lateral shelf on the quadrate.
57. The hyomandibular process that extends over the metapterygoid's posterodorsal region.
58. The presence of two or more intercostal ligaments that join the three or more of the anteriormost full pleural ribs.

The two subunits of the assemblage defined by characters 44 to 58 are, in turn, distinguished by their less inclusive sets of shared derived characters. These clades are (1) the morphologically diverse, speciose family Anostomidae; and (2) the Chilodontidae, a small group both in terms of genera and species, that is, characterized by numerous synapomorphies and relatively little intrafamilial variation.

#### FAMILY ANOSTOMIDAE

The family Anostomidae is largely characterized by branchial apparatus and suspensorium modifications that reflect the unique overall form of those systems in the family. The synapomorphies for the species of anostomids are as follows.

59. The expansion of the ascending process of the premaxillary resulting in a heavy triangular bone.
60. The pronounced expansion of the dentary replacement tooth trench, and the distinct fenestra along the ventral portion of the trench.
61. The enlargement of the dentary and premaxillary teeth.
62. The expansion of the third epibranchial's medial portion to form a curved process that extends medially over the fourth infrapharyngobranchial's dorsal surface.
63. The very well-developed cord-like ligament that runs between the lateral surface of the ectopterygoid and the ventral wing of the lateral ethmoid.
64. The distinct process on the posterolateral surface of the ectopterygoid.
65. The expansion of the preopercle's lateral surface to form a shelf for the origin of the adductor mandibulae.
66. The enclosure of the anterior portion of the preopercular laterosensory canal by two or three autogenous ossified tubes.
67. The quadripartite laterosensory canal system in the extrascapular.



68. The two or more intercostal ligaments that unite four or more of the anteriormost full pleural ribs.
69. The triangular, autogenous section of the levator arcus palatini that arises from the posterodorsal portion of the orbital cavity and inserts on the anterodorsal margin of the hyomandibula.
70. The subdivision of the A<sub>1</sub> portion of the adductor mandibulae.
71. The expansion of the posterior part of the A<sub>2</sub> portion of the adductor mandibulae medial of the levator arcus palatini and its partial origin on the hyomandibula.
72. The dorsal expansion anteriorly of the A<sub>3</sub> and A<sub>2</sub> portions of the adductor mandibulae that results in the contact of these muscles with each other dorsal to the tendon that attaches to the main body of A<sub>2</sub>.
73. The absence of the A<sub>w</sub> portion of the adductor mandibulae.

Anostomids are a distinctive group of some ten genera, a number of which are monotypic, but with *Leporinus* containing some 70 nominal species. Phylogenetic relationships within the subfamily Anostominae, which is characterized by some very unusual jaw adaptations, were analyzed by Winterbottom (1980), who also revised the contained species. Most of the remaining genera, particularly *Leporinus*, are poorly understood phylogenetically and taxonomically.

#### FAMILY CHILODONTIDAE

The members of the Chilodontidae have in common a profusion of synapomorphous modifications not encountered elsewhere in the families analyzed or often in any other fishes. Many of these characters are associated with the form of the epibranchial organ, which is not approximated in outgroups reported on in the literature or examined during this study. A second system that shows marked modifications is the pectoral girdle; perhaps as a consequence of the unusual head-down body orientation utilized by chilodontids while swimming. The various synapomorphies for members of the family are as follows.

74. The reduction in the relative size of the premaxilla.
75. The expansion in the relative size and thickness of the maxilla.
76. The ossified supramaxilla located along the posterodorsal margin of the maxilla.
77. The anteroventral expansion of the mesethmoid into an angled process that extends between the premaxillae.
78. The three or more cusps on all pharyngeal teeth.
79. The posteroventral expansion of ceratobranchial four into a broad, curved surface.
80. The expansion of the anterior portions of ceratobranchial five into a cup-shaped plate.
81. The rotation anteriorly of the tooth-bearing portion of ceratobranchial five.
82. The ridges on the dorsal surfaces of ceratobranchials 1, 2, and 3.
83. The reorientation posteriorly of the fifth upper pharyngeal tooth plate.
84. The pronounced transverse expansion of the third infrapharyngobranchial's posterior portion.
85. The ridges on the ventral surfaces of epibranchials 1, 2, and 3.
86. The posterior rotation of the ventral portion of the fourth epibranchial.
87. The lateral and dorsal expansion of the cartilaginous fifth epibranchial to form the major part of the anterior wall of the epibranchial organ.
88. The shell-shaped connective tissue sheet that extends dorsal to the fifth ceratobranchial and forms the posterior wall of the epibranchial organ.
89. The distinct ridges on the soft tissue layer that covers the adjoining surfaces of the fourth and fifth ceratobranchials.
90. The distinct band-like muscle on the anterior and posterior surfaces of the epibranchial organ.
91. The laterally thickened anterior and posterior ceratohyals with pronounced ridges along their lateral surfaces.
92. The complex, thickened interhyal with the ligament that extends to the metapterygoid

and quadrate attaching to the discrete medial process of the interhyal.

93. The ventral expansion of the main shaft of the supracleithrum.
94. The elimination of the ventral process and laterosensory canal bearing portion of the posttemporal and the anterior section of the extrascapular.
95. The direct articulation of the dorsal tip of the extrascapular with the pterotic.
96. The expansion of the posteroventral spine of the pterotic into a flat articular surface that contacts a corresponding supracleithral process.
97. The absence of postcleithrum 1.
98. The dorsal expansion of the proximal portions of the first three full pleural ribs.
99. The vertical expansion of the parapophyses and articular fossae associated with the first three full pleural ribs.

Very few of the shared derived characters common to the members of the family are readily visible externally. Consequently, chilodontids do not appear as highly derived superficially as do members of some of the other families in the suprafamilial lineage under discussion. Though very distinct anatomically, the group has not undergone any great intrafamilial differentiation or phyletic radiation. Two genera and three or four species presently are recognized (Géry, 1977b).

### Discussion

The advanced hypothesis of relationships is the most parsimonious derivable, given the available information on the polarity and distribution of characters in the examined body systems of curimatids, prochilodontids, anostomids, and chilodontids. The size and complexity of the Characiformes and scarcity of specimens of various taxa limits the practical outgroup comparisons. Thus, the occurrence of characters may in some cases be wider than noted here.

Two types of homoplasies were encountered: those internal to the four-family clade and convergencies between a subsection of that lineage

and one or more characiform outgroups. The majority of these incongruities are loss characters, while others are sufficiently different in the various groups that possess them to cause doubts about their homology.

Characters hypothesized to be homoplasiously distributed within the four-family unit are as follows.

1. The distinct lateral shelf on the quadrate in the Prochilodontidae and the unit that consists of the Anostomidae and Chilodontidae.
2. The autogenous ossified tubes associated with the anterior section of the preopercular laterosensory canal system in the Prochilodontidae and Anostomidae.
3. The absence of a dentary replacement tooth trench in the Chilodontidae and Curimatidae.
4. The longitudinal foreshortening of the lower jaw in the Prochilodontidae and the unit that consists of the Chilodontidae and Anostomidae.
5. The reduced teeth not in direct contact with the jaws in the Chilodontidae and Prochilodontidae.

Roberts (1973) also advanced the similarities in ethmoid (= mesethmoid) form and the enclosure of the angular (= retroarticular) by the dentary as indicators of close anostomid-prochilodontid relationships. The homology of these characters is difficult to evaluate. If they are homologous apomorphies they would be considered homoplasies under the results of this study. That decision and the comparable treatment of the five characters listed above are based on parsimony criteria. Including the two characters listed by Roberts, we find that three characters support a hypothesis of a sister group relationship between the Prochilodontidae and the Anostomidae (the two characters proposed by Roberts and character 2 above). Two characters (1 and 4 above) are congruent with the concept of the Prochilodontidae being most closely related to the lineage that consists of the Anostomidae and the Chilodontidae. One character (number 3 above) unites the Chilodontidae and Curimatidae. Finally, one character (number 5 above)

unites the Prochilodontidae and Chilodontidae. If we consider the tooth reduction of character 5 to be an intermediate state to the total loss of jaw dentition in the adults of the Curimatidae, a reduction or loss of jaw teeth would rather be a synapomorphy for the assemblage formed by the Prochilodontidae, Chilodontidae, and Curimatidae.

The acceptance of even the most corroborated of these phylogenetic alignments (that is, uniting the Prochilodontidae and the Anostomidae) would require the hypothesis that all 11 characters considered synapomorphous for the Curimatidae and Prochilodontidae arose independently in those two lineages and that a similar situation exists with respect to the 13 characters synapomorphous for the Anostomidae and Chilodontidae. The selection of a hypothesis of a sister group relationship between the Prochilodontidae and Anostomidae would indeed eliminate the three homoplasies noted above but would necessitate a hypothesis that 24 other characters arose independently; as such, it would be obviously less parsimonious. Comparable arguments are applicable to the other characters considered homoplasious in the present study.

Such criteria are also applicable to the question of the absence of the first postcleithrum in chilodontids and a subunit of anostomids, and the absence of an ossified first basibranchial in curimatids and some anostomids. Several characters considered synapomorphous for the members of the Anostomidae are evidently secondarily lost in *Gnathodolus* and perhaps its sister genus *Sartor*, which was not available for study (see "Suspensorium and Circumorbital Series"). Once again, parsimony arguments based on the available data on intra-anostomid relationships suggest that the absence of those characters within the Anostomidae is a secondary loss.

A variety of other characters were noted which evidently occur homoplasiously in the group that consists of the Curimatidae, Prochilodontidae, Anostomidae, and Chilodontidae or subunits of that clade and various characiform outgroups. These characiform outgroups include the Citharinidae, Parodontidae, and Hepsetidae, various

subunits of the Distichodontidae, the Hemiodontidae (particularly *Bivibranchia* and *Anodus*) and within the Characidae *Acestrorhynchus*, *Chalceus*, *Colossoma*, *Crenuchus*, *Hydrolycus*, *Rhaphiodon*, and the Gasteropelecinae. The characters involved, comments on their possible homology, and more specific details on their phylogenetic distributions are discussed in the preceeding "Character Description and Analysis". Neither the ingroup homoplasies nor those with characiform outgroups show a repeated pattern of phylogenetic distribution consistent with an alternative equally or more parsimonious hypothesis of relationships.

The majority of the noted outgroups have only one shared derived character in common with some subunit of the four-family assemblage analyzed. Hypotheses of relationships based on such characters are obviously less robust than that based on the more numerous characters listed in the previous section. Only two taxa, the Old World characiform family Citharinidae and the Neotropical genus *Anodus* show any multiple, derived similarities with subunits of the clade consisting of the Curimatidae, Prochilodontidae, Anostomidae, and Chilodontidae.

The loss of dentition on the fourth upper pharyngeal tooth plate is a characteristic of the Citharinidae and the entire four-family assemblage. The Citharinidae has a reduction or loss of lower pharyngeal dentition and the presence of an opercular flange in common with the Curimatidae plus Prochilodontidae. Both the Citharinidae and the Curimatidae have a third posttemporal fossa and possess a well-developed cartilagenous ethmoid block. An outwardly rotated dentary replacement tooth trench is shared by the Citharinidae and the Prochilodontidae. Finally, the Citharinidae and Chilodontidae have in common a secondary contact of the supracleithrum with a posteroventrally expanded process of the pterotic. Any hypothesis of a sister group relationship between the Citharinidae and any family or multifamilial grouping just listed would require the assumption that the various hypothesized synapomorphies for the Citharinidae and Distichodontidae (Vari, 1979) are actually homoplasies. In the majority of cases it would also necessitate

similar assumptions relative to the numerous synapomorphies for the unit that consists of the Curimatidae, Prochilodontidae, Anostomidae, and Chilodontidae or subgroups of that clade. Thus, for example, the recognition of the Citharinidae and Curimatidae as sister groups on the basis of their synapomorphous possession of a third posttemporal fossa and a large cartilagenous ethmoid block would necessitate the assumption that characters 1 through 15 are homoplasies. That procedure results in obviously less parsimonious hypotheses.

The second taxon, the genus *Anodus*, shares the absence of jaw teeth with the Curimatidae, the absence of lower pharyngeal teeth with the Curimatidae and Prochilodontidae, and the absence of teeth on the fourth upper pharyngeal tooth plate with the Curimatidae, Prochilodontidae, Anostomidae, and Chilodontidae. The hypothesis of a sister group relationship between *Anodus* and the four-family assemblage is incongruent with the various synapomorphies that unite the genus and the Hemiodontidae (Roberts, 1974). Any hypothesis of a close relationship between *Anodus* and subunits of the four-family clade is in addition incongruent with the various synapomorphies for and within that quadri-familial assemblage.

Uncertainties about the homology of the teeth on the prochilodontid suctorial mouth make it impossible to unambiguously evaluate the proper phylogenetic level at which it was appropriate to use the absence of maxillary teeth as a character in the phylogenetic reconstruction. The absence of teeth on that bone may be either a synapomorphy for the four-family unit or at broader or narrower levels of taxonomic universality. The reduced size of the jaw dentition in chilodontids and prochilodontids may be homologous, perhaps also representing an intermediate stage in a reductional trend, which achieves its terminal condition in the edentulous jaws of curimatids. The ambiguity associated with the question of homology in the character makes it impossible to determine the appropriate level at which to use the morphological information. Similarly, it is not possible to determine at what phylogenetic level

it is correct to use the various adaptations of the third postcleithrum in the Chilodontidae. The above characters, the analyses of polarities, and alternate scenarios consistent with their phylogenetic distribution were discussed in greater detail in preceding sections of this paper.

### Comparisons with Previous Classifications

A number of alternate taxonomic concepts have been proposed for the families Curimatidae, Prochilodontidae, Anostomidae, and Chilodontidae. Those treatments typically lack an explicit statement of the methodology of analysis and the phylogenetic assumptions underlying the classification. Rather, each of the previously proposed classifications is an amalgam of phenetic and quasi-phyletic concepts, with a consequent low retrievability of the underlying phylogenetic assumptions. Two exceptions, at least with respect to the last factor, were the studies of Eigenmann (1917) and Roberts (1973).

The differing classificatory schemes or phylogenetic hypotheses fall into five major patterns, arranged chronologically by first presentation (family concepts follow Greenwood et al., 1966).

1. The union of the Curimatidae, Prochilodontidae, Chilodontidae, and Parodontidae in one taxon and the separation of the Anostomidae in a second taxon of equivalent rank (Günther, 1864).
2. The placement of the Curimatidae and Prochilodontidae with the Citharinidae; the Anostomidae with some members of the Characidae and Lebiasinidae; and the Chilodontidae with the Hemiodontidae and Parodontidae (Boulenger, 1904).
3. The incorporation of the Curimatidae, Prochilodontidae, Anostomidae, and Chilodontidae into a single taxon (Regan, 1911; Gregory and Conrad, 1938).
4. The recognition of the Curimatidae, Prochilodontidae, Anostomidae, Chilodontidae, Hemiodontidae, and Anodinae as a discrete lineage (Eigenmann, 1917).
5. The union of the Curimatidae, Prochilodontidae and Chilodontidae as a taxon, distinct

from, but equivalent in rank to, that containing the Anostomidae (Géry, 1977b).

6. The hypothesis that the Prochilodontidae is not closely related to the Curimatidae but rather to the Anostomidae (? and Chilodontidae) (Roberts, 1973).

The degree to which phylogenetic concepts, if any, were incorporated into the majority of the above classificatory schemes is uncertain. Thus, it is only possible to note the utility, or lack thereof, of the previously suggested taxonomic subdivisions as appropriate indicators of the hypothesis of relationships arrived at in this study, given the criterion that all recognized taxa must be monophyletic. Eigenmann's (1917) hypothesis can reasonably be interpreted as a phyletic concept, although with a limited degree of resolution of relationships within his proposed lineage. Similarly, Roberts (1973) dealt with questions of relationship, although there is some question as to the exact hypothesis advanced.

Günther's (1864) Anostomina group, which consisted of what are now considered anostomids, is monophyletic according to the findings of this study. Prochilodontids, curimatids, and chilodontids, together with hemiodontids and parodontids, all were included in his Curimatina. Given the separation of anostomids into a separate group, as the Anostomina, Günther's Curimatina group is nonmonophyletic, in that it does not include all descendents of the hypothesized common ancestor of the lineage. Thus, Günther's classification is not an appropriate vehicle to convey the hypothesis of the relationships arrived at herein for the Curimatidae, Prochilodontidae, Anostomidae, and Chilodontidae. Furthermore, the Hemiodontidae, placed by Günther in the Curimatina group, shares various derived characters, including the presence of a rhinosphenoid and tooth form, with subunits of the Characidae, with which it is presumably most closely related. The exact phylogenetic placement of parodontids is not resolved, but available data fails to support the hypothesis that they are more closely related to the remaining members of Günther's Curimatina group than those taxa are to anostomids.

Boulenger's taxonomic scheme (1904) places subunits of the monophyletic four-family unit in three different taxa that each contain other characiform groups. His proposed classification is, thus, highly incongruent with the proposed phylogenetic history of the clade. Temporarily putting aside the works of Regan and of Gregory and Conrad, we can see that Eigenmann's more explicit phyletic statement agrees with that presented here in uniting curimatids, prochilodontids, chilodontids, and anostomids into a single lineage. Eigenmann did not, however, suggest what were the relationships among these four families. The limited internal resolution of his hypothesis restricts comparisons at lower levels of universality. Our present understanding of phylogenetic relationships within characiforms, indicates, however, that the Hemiodontidae and Anodinae, which he also aligned with those taxa, are actually more closely related to other phyletic subunits of the order.

Géry (1977b), in recognizing an Anostomidae for a group that consists of anostomids, and a Curimatidae formed by curimatids, chilodontids, and prochilodontids, nearly approximates Günther's classification; differing only in separating the Parodontidae into a separate taxon. Given the fact that his Curimatidae does not satisfy the primary criterion of this analysis—that it contains all the descendents of its hypothesized common ancestor—it is considered an invalid indicator of the hypothesis of relationships arrived at in this study.

Returning to the earlier classifications of Regan (1911) and Gregory and Conrad (1938), we see that their union of what are presently recognized as the Curimatidae, Anostomidae, Chilodontidae, and Prochilodontidae into a single taxon accurately reflects the monophyly of the group other than for the inclusion of the genus *Anodus*, which is apparently more closely related to the Hemiodontidae (Roberts, 1974). These works are the only previous studies that utilized a classificatory scheme under which nearly all recognized taxa constitute monophyletic assemblages under the results of this study. Gregory and Conrad (1938) were not explicit about their concepts of relation-

ships within the four-family lineage. Therefore, comparisons cannot be made at lower levels of universality between their scheme and the hypothesis advanced in this study. Other than for the aforementioned inclusion of *Anodus* in the Curimatinae by Regan, his classification agrees with the phylogenetic hypothesis advanced herein both at the level of the four-family unit and at lower levels of universality. Regan did not comment on the possible relationships of the four-taxon group to other characiforms, whereas Gregory and Conrad made a qualified suggestion that the assemblage formed by these four families was most closely related to the Citharinidae (sensu Greenwood et al., 1966). The numerous synapomorphies for citharinids and distichodontids (Vari, 1979) indicate that Gregory and Conrad's suggestion is incongruent with available data on characiform phylogeny.

Regan united the taxa as a family with three subfamilies, whereas Gregory and Conrad considered them to form a subfamily. More recently each of the components has been recognized as a full family (Greenwood et al., 1966). It is, of course, presently impossible to be non-arbitrary in the decision as to which taxonomic level is the most appropriate for the entire assemblage or its subunits given a possible range between a single subfamily and four families. Such a decision must await a phylogenetic hypothesis of this clade's placement within characiforms. The recognition of four separate families in this study is in keeping with the general practice of most recent works. Suprafamilial taxa for more inclusive groupings are not proposed at this time because of our still preliminary concepts of higher level relationships within the Characiformes.

It was noted earlier that Roberts' treatment (1973) of the Prochilodontidae was the one work to advance phylogenetic concepts for at least portions of the four-family assemblage. Roberts, without specific cross-reference, commented that earlier researchers had proposed a close relationship between the Curimatidae and Prochilodontidae. His primary premise, in contrast, was that the relationships of prochilodontids lie with groups other than curimatids. Some ambiguity

exists on the identity of the specific group or groups he considered the closest relatives to the prochilodontids. In the abstract to his work (1973:213) he stated that prochilodontids "are closely related to Anostomidae and Chilodontidae," whereas in his discussion of relationships (1973:221) he stated that "the evidence favoring relationship between Prochilodontidae and Anostomidae is relatively strong." The latter, more limited concept of the sister group to prochilodontids is that discussed at greatest length in the paper and, thus, presumably more in keeping with the ideas of the author. Both concepts of outgroup relationship run counter to the results of this study. The hypothesis that prochilodontids are phylogenetically aligned with the lineage that consists of anostomids and chilodontids would necessitate the especially unparsimonious hypothesis of repeated convergent acquisitions in the Curimatidae and Prochilodontidae of all eleven of the characters herein considered synapomorphies for the members of the curimatid-prochilodontid clade. The more restricted hypothesis of relationships that uses the Anostomidae as the sister group to the Prochilodontidae would involve both those concepts of convergence and the independent acquisition in the Chilodontidae and Anostomidae of the numerous derived characters considered synapomorphies for that bifamilial lineage in this study. Thus, both of the two possible sister group concepts mentioned by Roberts are significantly less parsimonious than the hypothesis of relationship arrived at in this study.

### Resumen

Una hipótesis acerca de las relaciones filogenéticas de las familias Curimatidae, Prochilodontidae, Anostomidae, y Chilodontidae pertenecientes al Orden Characiformes es presentada, utilizando la metodología de la sistemática filogenética (cladística) propuesta por Hennig (1950). Numerosos caracteres derivados (apomórficos), compartidos por estas cuatro familias, fueron encontrados en las mandíbulas, arcos branquiales, suspensorium, neurocraneo, columna vertebral, y musculatura de la cabeza. Los resultados

de este estudio indican que los Curimatidae están más cercanamente relacionados con los Prochilodontidae. La unidad formada por estas dos familias es a su vez el grupo hermano (sister group) de la unidad formada por las familias Anostomidae y Chilodontidae. Se encontraron también una serie de caracteres únicos (autapomorfias), que definen a estas familias como unidades monofiléticas.

La hipótesis de relaciones desarrollada en este sentido rechaza la sugerencia presentada por Roberts (1973:221) la cual establece que los Prochilodontidae están más cercanamente relacionados con la familia Anostomidae, que a los Curimatidae. Boulenger (1904) reunió los Curimatidae y Prochilodontidae con la familia de characiformes africanos Citharinidae. Los datos obtenidos en este estudio y el trabajo previo de Vari (1979) indican que el criterio de Boulenger crea un taxón no-natural. Günther (1864) y Géry (1977a) erigieron un taxón para incluir Anostomidae y otro taxón de rango equivalente para los Curimatidae, Prochilodontidae, y Chilodontidae. Según el criterio de este estudio, el último taxón propuesto por los citados autores es no-monofilético y no refleja la historia evolutiva de este grupo de familias. El concepto de relaciones filogenéticas llevadas adelante por Eigenmann (1917) esta de acuerdo con la filogenia hipotética propuesta en este estudio. Sin embargo, Eigenmann incluye a los Hemiodontidae en su discusión, grupo que es excluido en este trabajo. Roberts (1974) sugiere que el género *Anodus* (un characiforme sin dientes) no está cercanamente relacionado con los Curi-

matidae, a pesar de la larga tradición taxonómica la cual asocia estos taxa. En este estudio, la inclusión de *Anodus* en la familia Curimatidae esta apoyada por varios caracteres derivados compartidos (sinapomorfias).

Tres formas diferentes de órganos epibranchiales (bien desarrollados) han sido determinados en los Characiformes. Los Curimatidae y Prochilodontidae tienen un órgano epibranchial parecido a un gran saco muscular, mientras que los de la familia africana Citharinidae son altamente divididos y soportados por una serie de pequeñas osificaciones. El órgano epibranchial en Chilodontidae está formado por una extensión cartilaginosa de quinto epibranchial, una banda de tejido conectivo asociado al cuarto epibranchial y partes del cuarto y quinto ceratobranchiales. Las diferencias morfológicas entre estos tres tipos de paquetes faríngeos y los datos disponibles sobre las interrelaciones de los Characiformes indican que órganos epibranchiales bien desarrollados, han evolucionado separadamente, al menos tres veces, dentro de este Orden. Esta conclusión esta de acuerdo con la hipótesis previa de Nelson (1967) quien sugirió que los órganos epibranchiales desarrollados aparecieron independientemente en diferentes grupos de peces. Bertmar, Kapoor, y Miller (1969) en contraste, consideraron que estos órganos son ancestrales para los peces teleosteos, cuya ausencia en muchas líneas evolutivas sería debido a pérdidas secundarias. Los resultados de este estudio indican que esta última hipótesis no es parsimoniosa cuando es aplicada al Orden Characiformes.

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