A Phylogenetic Study of the Neotropical Characiform Family Curimatidae (Pisces: Ostariophysi)

RICHARD P. VARI

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ABSTRACT

Vari, Richard P. A Phylogenetic Study of the Neotropical Characiform Family Curimatidae (Pisces: Ostariophysi). *Smithsonian Contributions to Zoology,* number 471, 71 pages, 45 figures, 3 tables, 1989.—Osteology and soft anatomy of the species of Curimatidae were studied to examine the hypothesis that the family is monophyletic, and to advance a hypothesis of phylogenetic relationships within the family.

Features of the branchial apparatus, buccopharyngeal complex, hyoid arch, jaws, palatine arch, and neurocranium corroborate the monophyly of the Curimatidae. Additional characters in a subset of these systems are congruent with the hypothesis of a sister group relationship between the Curimatidae and Prochilodontidae (Vari, 1983). Shared derived characters of those systems and the antorbital, infraorbitals, opercular apparatus, ligamentum primordiale, hypural complex, caudal-fin rays, proximal pterygiophores of the dorsal fin, laterosensory canal systems of the head and body, and squamation define phylogenetic subunits of the Curimatidae, supporting a phylogenetic hypothesis of four sequential dichotomies and a terminal polychotomy.

I recognize eight genera in the Curimatidae. *Curimatopsis, Potamorhina, Curimata, Psectrogaster, Steindachnerina, Pseudocurimata,* and *Curimatella* are each hypothesized as monophyletic on the basis of additional shared derived characters. No unique derived characters were found to define the eighth recognized genus, *Cyphocharax.*

Curimatichthys Fernández-Yépez (1948) is a synonym of *Curimatopsis. Potamorhina* is redefined to include *Gasterotomus* Eigenmann (1910), *Gasterostomus* Fernández-Yépez (1948), *Suprasinelepichthys* Fernández-Yépez (1948), and *Potamorrhina* Braga and Azpelicueta (1983). *Curimata* Bosc (1817) has nine junior synonyms: *Semitapicis* Eigenmann and Eigenmann (1889b); *Peltapleura* Fowler (1906); *Acuticurimata* Fowler (1941); *Allenina* Fernández-Yépez (1948); *Lambepiedra* Fernández-Yépez (1948); *Bitricarinatra* Fernández-Yépez (1948); *Bondichthys* Whitley (1953); *Stupens* Whitley (1954); and *Semitapiscis* Braga and Azpilicueta (1983). Three genera are included in *Psectrogaster*: *Pseudopsectrogaster* Fernández-Yépez (1948), *Hamatichthys* Fernández-Yépez (1948), and *Semelcarinata* Fernández-Yépez (1948). *Rivasella* and *Curimatorbis,* both proposed by Fernández-Yépez (1948), are synonyms of *Steindachnerina* Fowler (1906). *Curimatella* has three junior synonyms, all described by Fernández-Yépez (1948): *Apolinarella, Walbaunina,* and *Lepipinna. Cyphocharax* has four synonyms: *Xyrocharax* Fowler (1913b), *Hemicurimata* Myers (1929), *Curimatoides* Fowler (1940), and *Cruxentina* Fernández-Yépez (1948).

The hypothesis of intrafamilial phylogenetic relationships described herein is incongruent, to differing degrees, with classificatory schemes proposed by Eigenmann and Eigenmann (1889b), Eigenmann (1910), Fowler (1975), and Géry (1977b). Numerous differences exist at all taxonomic levels between the scheme of relationships proposed in this study and the "phylogenetic tree" put forward by Fernández-Yépez (1948). Additional hypothesized derived characters described herein are in agreement with the reassignment of *Anodus* Spix, 1829 (in Spix and Agassiz, 1829) and *Eigenmannina* Fowler (1906) from the Curimatidae to the Hemiodontidae, first proposed by Roberts (1974) and congruent with results of Vari (1983).

Homoplasious characters are discussed in terms of their overall taxonomic distributions, and relative to their innovative versus reductive natures. Reductive features involving the degree of development of the laterosensory canal system were found to be convergent between *Curimatopsis* and a subset of *Cyphocharax.* These paedomorphic features are evidently a consequence of the relative size reduction of these species compared to proximate outgroups.

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Contents

A Phylogenetic Study of the Neotropical Characiform Family Curimatidae (Pisces: Ostariophysi)

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Introduction

The 100 or more species of the Neotropical characiform family Curimatidae inhabit a broad range of freshwater ecosystems from the still ox-bow lakes, slow-flowing streams, and meandering rivers typical of lowland floodplains, to swift tributaries and rapids of the Andean piedmont and the uplands of the Guayanan and Brazilian shields. Curimatids are components of the ichthyofauna of trans-Andean Pacific drainages of Central and South America from southern Costa Rica (Bussing, 1966:221) to northern Peru (Eigenmann, 1922:104; Ortega and Vari, 1986:11), and along that versant they also inhabit the Caribbean drainages in northwestern South America (most notably the Río Magdalena system and the Lago Maracaibo drainage basin). Curimatid species occur in the vast portion of South America to the east of the Andes, including the numerous rivers from the Río Orinoco system in Venezuela to south of Buenos Aires, Argentina.

Within this extensive geographic range, the most speciose curimatid fauna is that of the Rio Amazonas basin, inhabited by over 40 curimatid species representing all of the major phyletic lineages of the family. The Río Orinoco and Río Paraguay-Paraná systems include over a dozen species of the family within each of their ichthyofaunas. Less speciose curimatid assemblages are found in Lago Maracaibo, the rivers of the Atlantic slopes of the Guianas, the rivers of coastal Brazil, Uruguay, and central Argentina, and in the Caribbean and Pacific drainages of trans-Andean South and Central America.

The speciose nature of the Curimatidae is reflected in their variability of overall body size and form. A nearly ten-fold range in standard length (SL) is found between the largest known adult males of *Curimatopsis evelynae* Géry (ca. 33 mm SL) and the largest reported *Curimata mivartii* Steindachner (320 mm SL, Dahl, 1971:105). The range in body form within the family is represented at one extreme by elongate fusiform species such as *Curimata ocellata* Eigenmann and Eigenmann (Figure 1) of the Amazon basin, which schools with and mimics hemiodontids (Géry, 1977a). At the other extreme, *Psectrogaster abramoides* (Kner) is a deep bodied, laterally compressed species also from the Amazon (Figure 2). The majority of curimatid species cluster around an intermediate, moderately compressed and slightly elongate body form typified by *Curimata incompta* Vari (Figure 3), a species endemic to the Río Orinoco system.

Despite the poor representation of some members of the family in systematic collections, many curimatid species occur in large schools (Santos et al., 1985:28-29) that constitute a significant proportion of fish biomass in riverine and lacustrine ecosystems (Lowe-McConnell, 1975:109). In those localities, they exploit the floculent organic material, microdetritus, microvegetation, and filamentous algae typical of most Neotropical aquatic habitats (Carvalho, 1984; Nomura and Hayashi, 1980; Nomura and Taveira, 1979). The populations of numerous curimatid species are particularly concentrated during spawning migrations such as the "piracema" of the Rio Mogi-Guassu of southeastern Brazil (de Godoy, 1975:581-603). These seasonal concentrations permit the ready exploitation of those species by commercial and subsistence fisheries throughout most of the distributional range of the family (Mago-Leccia, 1970:31; Dahl, 1971:105; Rodriquez, 1973; Lowe-McConnell, 1975:74; Saint-Paul and Bayley, 1979:112; Smith, 1981:140; Goulding, 1981:60). Curimatids are also important food items for larger, commercially important, predatory fish species.

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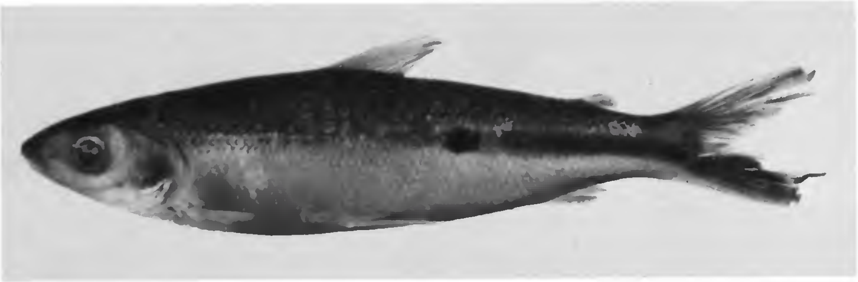

FIGURE 1.—*Curimata ocellata*, USNM 267973, 160.3 mm SL, Brazil, Amazonas, Rio Marauia.

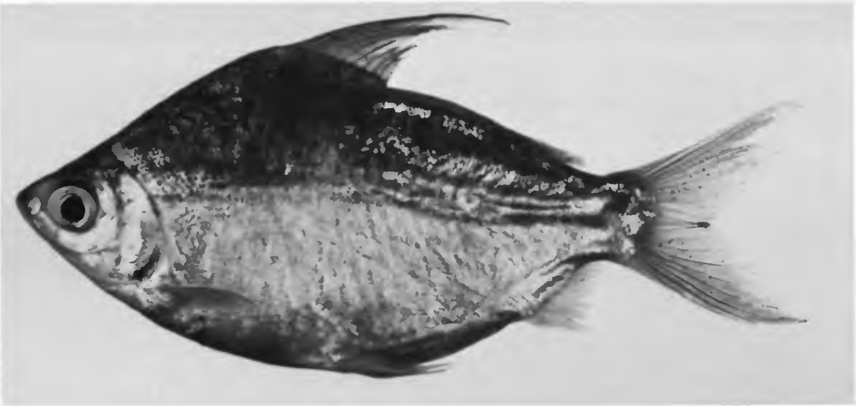

FIGURE 2.—*Cyphocharax abramoides*, USNM 267952, 105.8 mm SL, Brazil, Pará, Rio Xingu, Belo Monte.

FIGURE 3.—*Curimata incompta*, USNM 273308, 81.2 mm SL, Venezuela, Estado Bolivar, still backwater off Río Orinoco at El Burro.

The diversity of curimatids, particularly the larger species, have been long known to science. More than two centuries ago both Linneaus (1758:312; 1766:514) and Gronovius (1763:123) listed several nominal forms brought to Europe from northeastern South America. Geographically and ecologically more encompassing ichthyological collecting efforts in Neotropical freshwaters since the middle of the eighteenth century have brought curimatids of additional phyletic lineages to the attention of systematists. This greater availability of curimatid specimens from all regions of South America resulted in a progressive increase of described species, with over 120 nominal species or subspecies proposed to date. Associated with the increasingly complex species-level taxonomy were the proposals of numerous genera and subgenera. Despite these efforts, uncertainty continued to pervade curimatid taxonomy at both the specific and supraspecific levels.

The multitude of species level problems within the Curimatidae remained unsettled, partially as a consequence of the absence of a broad overview of the group; most treatments were limited to geographically or politically circumscribed regions. These arbitrary limitations hindered elucidation of species level problems, resolution of which required analysis of geographic and taxonomic samples. The majority of authors were further handicapped by absence of detail in many of the original species descriptions, and by limited collections of comparative materials. These factors, compounded by the large number of nominal species of curimatids, resulted in uncertainty as to the number of recognizable species of curimatids, a poor understanding of the distinguishing characters of the recognizable forms, and confusion as to the geographic distributions of those taxa. Revisionary studies completed (Vari, 1982a,b, 1984a,b, 1987; Vari and Géry, 1985; Vari and Nijssen, 1986) and in progress focus on questions of specific limits and geographic distributions. Such problems are not pursued further in this paper.

Research on the second central problem in curimatid taxonomy, the sequence of evolutionary events within the family, has lagged behind analyses of species-level questions. The relatively few studies that attempted, at least to some degree, to address intra-familial phylogeny failed to clarify our understanding of this core question. Those endeavors (e.g., Fernández-Yépez, 1948) typically made little attempt to critically examine the correlation, or lack thereof, between recognized supraspecific taxa and hypothesized lineages within the family. Rather, these studies usually proposed new genera and subgenera based, either explicitly or by default, on degrees of overall similarity or difference. In retrospect the weakness of such a quasi-phenetic system is reflected both in the erroneous specific and generic synonymizations that riddled the taxonomy of the family, and in the inappropriate assignment of species to supraspecific taxa. These factors led to differing views as to the composition of generic and suprageneric groupings within the Curimatidae.

The generic level subdivision of the family has proceeded in an episodic fashion during the last two centuries. Researchers prior to 1876 typically used *Curimatus* for the vast majority of curimatids (*Curimatus* is equivalent to *Curimata* Bosc, see Opinion 772, International Commission of Zoological Nomenclature, 1966). The only exception was the erroneous utilization of *Anodus* Spix for some members of the family (e.g., *Anodus latior* Spix, 1829 (in Spix and Agassiz, 1829) = *Potamorhina latior*, see Vari, 1984a). As noted by Roberts (1974:429), *Anodus* is not available in the Curimatidae, being properly applied to two species within the Hemiodontidae (see "Synapomorphy List and Phylogenetic Reconstruction"). Steindachner (1876:81) initiated the valid generic level subdivision of the Curimatidae when he advanced *Curimatopsis* as a subgenus of *Curimata* for the first species of curimatid known to retain an incompletely pored laterosensory canal as an adult. Cope (1878:675) continued this trend towards increased generic diversity with his description of the then monotypic genus *Potamorhina* for the distinctly modified species *Curimatus* (*Anodus*) *pristigaster* previously described by Steindachner (1876:73). The number of available nominal genera and subgenera within the family underwent a slow but progressive increase during the next seven decades in the publications of the following authors: Eigenmann and Eigenmann, who proposed *Psectrogaster* (1889a:7), *Curimatella* (1889b:415), and *Semitapicis* (1889b:417); Fowler, who created *Cyphocharax*, *Steindachnerina*, *Peltapleura* (1906:297-300), *Xyrocharax* (1913b:673), *Curimatoides* (1940:255), and *Acuticurimata* (1941:162); Eigenmann (1910:422), who described *Gasterotomus*; and Myers, (1929:620) who first used *Hemicurimata*. Fernández-Yépez (1948), in an outburst of generic subdivision, more than doubled the number of nominal genera and subgenera that were available prior to his study. His newly proposed genera (*Allenina*, *Apolinarella*, *Bitricarinata*, *Bondia*, *Camposella*, *Cruxentina*, *Curimatichthys*, *Curimatorbis*, *Hamatichthys*, *Lambepiedra*, *Lepipinna*, *Pseudocurimata*, *Pseudopsectogaster*, *Rivasella*, *Semelcarinata*, *Suprasinelepichthys*, and *Walbaunina*) brought the number of generic level names proposed for curimatids to thirty-one. Two of the genera proposed by Fernández-Yépez (1948), *Bondia* and *Camposella*, were replaced with *Bondichthys* and *Camposichthys* by Whitley (1953:134) who pointed out that they were already occupied in other groups. *Camposichthys* also proved to be preoccupied, and Whitley (1954:30) put forward *Stupens* as a substitute.

This trend towards generic level subdivision of the Curimatidae, most notably by Fernández-Yépez (1948), did little to resolve questions of interrelationships within the family at either specific or supraspecific levels. Ten of the twenty-seven genera recognized by Fernández-Yépez were monotypic and could not serve as indicators of phylogenetic relationship. The other more speciose genera proposed or recognized by Fernández-Yépez were nearly always ambiguously defined, with resultant uncertainties about generic limits and species assignment, difficulties previously commented upon by Böhlke

(1958:106). Attempts to resolve the problems prevalent in the classification proposed by Fernández-Yépez resulted in the subsequent shifting of species between nominal genera (Böhlke, 1958:108; Ringuelet et al., 1967:198; Britski, 1969:203; Vari, 1982a:12, 1984a:11).

Questions of generic diagnosis and inclusiveness aside, we nonetheless find that most authors who proposed classifications for the family or its subunits did so without discussion of the concepts, phenetic or phylogenetic, underlying their schemes. That inexactitude inhibited evaluation of underlying evolutionary patterns hypothesized for the family as a whole or in part, and obscured the degree to which the classifications attempted to reflect a conceptual basis.

The single equivocal exception, the nomenclatural system advanced by Fernández-Yépez and reflected in his "phylogenetic tree" (1948, fig. 12), represented an amalgam of phenetic and quasi-phylogenetic concepts based on a few relatively labile characters analyzed neither in terms of evolutionary polarity nor relative to their utility as indicators of phylogenetic relationship. Indeed Fernández-Yépez's (1948) "phylogenetic tree" is a visual representation of his dichotomous key to the genera of the family rather than a phylogenetic scheme.

The generic level subdivision of the family by Fernández-Yépez (1948), although extreme, nonetheless exemplifies the problems inherent in most classifications of the Curimatidae. Phenetically distinctive species or species groups were typically recognized as separate genera without consideration of the consequence of such actions on the phylogenetic naturalness (sensu Wiley, 1981:71) of previously recognized taxa. Residual species, under such procedures, in most instances formed non-monophyletic generic assemblages not delimited by uniquely derived characters. Rather, those taxa were characterized by combinations of primitive characters (symplesiomorphies) and did not delimit complete evolutionary lineages. As such they did not constitute valid units for comparative studies: morphological, biogeographic, or otherwise.

The studies reported in this paper were undertaken in order to advance a uniform hypothesis of higher level phylogenetic relationships within the Curimatidae based on discrete derived characters. Such a framework will provide a comparative context for future studies of the family, serving as the basis for comprehensive revisionary studies of subunits of the family and analyses of biogeographic patterns within the Curimatidae.

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Systematic Procedures

Phylogenetic relationships within the Curimatidae are analysed 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 series of nested, hierarchical units that reflect the best estimate of their evolutionary history.

Taxa are grouped on the basis of the possession of shared derived characters (synapomorphies). Such characters are considered the only valid basis for cladistic hypotheses of common ancestry. Hypotheses of relationship advanced on the basis of the common possession of shared primitive characters (symplesiomorphies), together with phylogenetic speculations based on concepts of overall phenetic similarity, or degrees of difference are either not useful methods for evaluating alternative phylogenetic hypotheses, or are incongruent with the aims of this study—the advancement of hypotheses of phylogenetic relationships within the Curimatidae. 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. Here, a computer algorithm, PAUP (Swofford, 1985), is employed to ensure maximum parsimony.

This does not assume that evolutionary mechanisms are necessarily parsimonious, but only that parsimony (simplicity) is the best available inferential principle (Beatty and Fink, 1979; Wiley, 1981). Monophyletic groups are defined as consisting of a hypothesized common ancestor of the lineage and all of its descendants. Traditional alternative definitions of monophyly (see summaries in Wiley, 1981) are of such generality as to include all possible combinations of subunits within a lineage, or are dependent on arbitrary taxonomic ranks, or both, and are therefore often meaningless in application and information content.

Character polarity (plesiomorphy vs. apomorphy; primitive vs. derived) is determined by outgroup comparisons, or via data from ontogenetic transformations, or both. Vari (1983:46-50) suggested that the Curimatidae is the sister group of the Prochilodontidae and the lineage formed by those two families is most closely related to that consisting of the Anostomidae and Chilodontidae. For purposes of character polarity determinations within the Curimatidae, outgroup comparisons are centered first on the Prochilodontidae and then on the Anostomidae and Chilodontidae. Comparisons to other, distantly related, characiform groups, both Neotropical and Old World, were undertaken in instances where outgroup comparisons to the three noted phylogenetically proximate families provided equivocal data on character polarity. Such broader outgroup comparisons were also carried out when the character in question in each of the proximate outgroup taxa was, in turn, uniquely derived relative to the generalized condition of characiforms and thus an inappropriate approximation of the hypothesized plesiomorphous condition of the character for characiformes. Conflicts between polarity decisions based on outgroup comparisons and those arrived at from ontogenetic data are analyzed within the context of the overall phylogeny. Discussions of the theory and methods of character polarity determination can be found in Wiley (1981), Watrous and Wheeler (1981), and Maddison et al. (1984).

Methods and Materials

Osteological and cartilaginous skeletal systems were examined in specimens cleared and counterstained for cartilage and bone with alizarin Red S and alcian blue following the methods outlined by Taylor and Van Dyke (1985). Previously cleared specimens stained solely in alizarin Red S, along with dry skeletal materials, were supplemental sources of osteological data. Anatomical illustrations were prepared using a Zeiss microscopic camera lucida.

TERMINOLOGY.—Myological terminology follows that of Winterbottom (1974). Osteological nomenclature is that of Weitzman (1962) with the following modifications. Vomer is substituted for prevomer, and intercalar for opisthotic. The element traditionally termed the epihyal is instead referred to as the posterior ceratohyal. The ceratohyal of many previous authors is more accurately termed the 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.

Unless otherwise noted, the concepts of the characiform families used in this paper are those of Greenwood et al. (1966) with three 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. (1966) is placed within the Distichodontidae following Vari (1979). Contrary to most previous authors, the Curimatidae of this study does not include the genera *Anodus* Spix and *Eigenmannina* Fowler, which are considered to be members of the Hemiodontidae after Roberts (1974). The higher level classification of the Ostariophysi follows Fink and Fink (1981). The nomenclature for the African members of the Characidae is that proposed by Paugy (1984:140–183).

The introductory discussion alluded to the complexity of the taxonomic schemes that have been applied to supraspecific subunits of the Curimatidae. The confusion engendered by the availability of over thirty generic level taxa and eight suprageneric groupings within the family is compounded by questions of species recognizability, errors in the morphological characterization of generic type species by Eigenmann and Eigenmann (1889b) and Fernández-Yépez (1948) (see Vari, 1984a:13–16, 25), and the presence of a number of undescribed species in the family. The resolution of many of these problems is the subject of revisionary studies published (Vari, 1982a,b, 1984a,b, 1987; Vari and Géry, 1985; Vari and Nijssen, 1986) and in progress. The numerous monotypic genera, many of which will not be recognized when revisionary studies are completed, makes resolution to the level of all nominal genera unproductive. The following discussion therefore deals with what would have constituted multigeneric assemblages under many previous classificatory schemes, particularly that of Fernández-Yépez (1948). The reduced number of recognized groups either represents taxonomic changes already proposed (Vari, 1982a, 1984a), or reflects the likely eventual classificatory schemes that will be proposed on the basis of research in progress. Table 1 lists the generic complexes used in this paper and the nominal genera that each incorporates. The assignment of the nominal species in the Curimatidae to the recognized genera is detailed in Tables 2

TABLE 1.—Genera recognized in this study, their included nominal genera, and the type species of those genera. Authors and date of description given for genera and type species of each genus.

Recognized genus	Included nominal genera and their type species
Curimatopsis	*Curimatopsis* Steindachner, 1876; *Curimatus (Curimatopsis) macrolepis* Steindachner, 1876 *Curimatichthys* Fernández-Yépez, 1948; *Curimatopsis microlepis* Eigenmann and Eigenmann, 1889a
Potamorhina	*Potamorhina* Cope, 1878; *Curimatus (Anodus) pristigaster* Steindachner, 1876 *Gasterotomus* Eigenmann, 1910; *Anodus latior* Spix, 1829 (in Spix and Agassiz, 1829) *Gasterostomus*.—Fernández-Yépez, 1948 [incorrect subsequent spelling of *Gasterotomus*] *Suprasinelepichthys* FernándezYépez, 1948; *Curimatus laticeps* Valenciennes, 1849 (in Cuvier and Valenciennes, 1849) *Potamorrhina* Braga and Azpelicueta, 1983 [unjustified emendation of *Potamorhina*]
Curimata	*Curimata* Bosc, 1817; *Salmo edentulous* Bloch, 1794 *Semitapicis* Eigenmann and Eigenmann, 1889b; *Charax planirostris* Gray, 1854 *Peltapleura* Fowler, 1906; *Salmo cyprinoides* Linnaeus, 1766 *Acuticurimata* Fowler, 1941; *Curimatus macrops* Eigenmann and Eigenmann, 1889b *Allenina* Fernández-Yépez, 1948; *Curimata murieli* Allen, 1942 (in Eigenmann and Allen, 1942) *Lambepiedra* Fernández-Yépez, 1948; *Lambepiedra alleni* Fernández-Yépez, 1948 *Bitricarinata* Fernández-Yépez, 1948; *Curimatus schomburgkii* Günther, 1864 *Bondichthys* Whitley, 1953; *Curimatus mivartii* Steindachner, 1878 *Stupens* Whitley, 1954; *Curimatus simulatus* Eigenmann and Eigenmann, 1889b *Semitapiscis* Braga and Azpelicueta, 1983 [unjustified emendation of *Semitapicis*].
Psectrogaster	*Psectrogaster* Eigenmann and Eigenmann, 1889a; *Psectrogaster rhomboides* Eigenmann and Eigenmann, 1889a *Pseudopsectrogaster* Fernández-Yépez, 1948; *Psectrogaster curviventris* Eigenmann and Kennedy, 1903 *Hamatichthys* Fernández-Yépez, 1948; *Anodus ciliatus* Müller and Troschel, 1845 *Semelcarinata* Fernández-Yépez, 1948; *Curimatus rutiloides* Kner, 1859
Steindachnerina	*Steindachnerina* Fowler, 1906; *Curimatus trachystetus* Cope, 1878 *Rivasella* Fernández-Yépez, 1948; *Curimatus melaniris* Fowler, 1940 *Curimatorbis* Fernández-Yépez, 1948; *Curimatus atratoensis* Eigenmann, 1912b
Pseudocurimata	*Pseudocurimata* Fernández-Yépez, 1948; *Curimatus lineopunctatus* Boulenger, 1911
Curimatella	*Curimatella* Eigenmann and Eigenmann, 1889b; *Curimatus lepidurus* Eigenmann and Eigenmann, 1889a *Apolinarella* Fernández-Yépez, 1948; *Curimatus meyeri* Steindachner, 1882a *Walbaunina* Fernández-Yépez, 1948; *Curimatus dorsalis* Eigenmann and Eigenmann, 1889b *Lepipinna* Fernández-Yépez, 1948; *Anodus alburnus* Müller and Troschel, 1845
Cyphocharax	*Cyphocharax* Fowler, 1906; *Curimatus spilurus* Günther, 1864 *Xyrocharax* Fowler, 1913b; *Curimata stigmaturus* Fowler, 1913b *Hemicurimata* Myers, 1929; *Curimata esperanzae* Myers, 1929 *Curimatoides* Fowler, 1940; *Curimatoides ucayalensis* Fowler, 1940 *Cruxentina* Fernández-Yépez, 1948; *Curimata hypostoma hastata* Allen, 1942 (in Eigenmann and Allen, 1942)

and 3. Revisionary studies have been published for two of the clades, *Curimatopsis* (Vari, 1982a,b) and *Potamorhina* (Vari, 1984a), and the nomenclature and synonymies of those revisions is followed in this paper. Since such revisions have not yet been published for the other lineages in the family, the discussion of the species in those taxa will be based on all the nominal species assignable to those lineages without prejudging which species will be recognized as valid in future studies.

Each synapomorphy is assigned a number in order to facilitate cross reference between the descriptive text, the listing in "Synapomorphy List and Phylogenetic Reconstruction," and the cladograms (Figures 44, 45), except that synapomorphies used exclusively within the genus *Curimatopsis* are assigned letters (A-K), for reasons explained in the text. Synapomorphy numbering is sequential in the final synapomorphy listing rather than in the descriptive text in order to simplify the discussion within "Synapomorphy and Phylogenetic Reconstruction." The synapomorphies, their polarities, and other comments are described in greatest detail within "Character Description and Analysis."

TABLE 2.—Genera recognized in this study and their contained nominal species, subspecies, and varieties. Species, subspecies, and varieties are listed chronologically within genera and are cited as in their original descriptions, with authors and dates of description.

Recognized genus	Included species
Curimatopsis	*Curimata (Curimatopsis) macrolepis* Steindachner, 1876
	Curimatopsis microlepis Eigenmann and Eigenmann, 1889a
	Curimatopsis macrocephalus Ahl, 1931
	Curimatopsis evelynae Géry, 1964a
	Curimatopsis crypticus Vari, 1982a
	Curimatopsis myersi Vari, 1982b
Potamorhina	*Anodus latior* Spix, 1829 (in Spix and Agassiz, 1829)
	Curimatus laticeps Valenciennes, 1849 (in Cuvier and Valenciennes, 1849)
	Curimatus (Anodus) pristigaster Steindachner, 1876
	Curimatus altamazonicus Cope, 1878
	Semitapiscis squamoralevis Braga and Azpelicueta, 1983
Curimata	*Salmo immaculatus* Linnaeus, 1758
	Salmo cyprinoides Linnaeus, 1766
	Salmo edentulus Bloch, 1794
	Charax planirostris Gray, 1854
	Curimatus vittatus Kner, 1859
	Curimatus schomburgkii Günther, 1864
	Curimatus asper Günther, 1868
	Curimatus knerii Steindachner, 1876
	Curimatus mivartii Steindachner, 1878
	Curimatus ocellatus Eigenmann and Eigenmann, 1889b
	Curimatus simulatus Eigenmann and Eigenmann, 1889b
	Curimatus macrops Eigenmann and Eigenmann, 1889b
	Curimata copei Fowler, 1906
	Curimatus semitaeniatus Steindachner, 1917
	Psectrogaster cisandina Allen, 1942 (in Eigenmann and Allen, 1942)
	Curimata murieli Allen, 1942 (in Eigenmann and Allen, 1942)
	Lambepiedra alleni Fernández-Yépez, 1948
	Curimata cerasina Vari, 1984b
	Curimata incompta Vari, 1984b
	Curimata species A (Vari, in press)
	Curimata species B (Vari, in press)
Psectrogaster	*Anodus ciliatus* Müller and Troschel, 1845
	Curimatus rutiloides Kner, 1859
	Curimatus essequibensis Günther, 1864
	Psectrogaster rhomboides Eigenmann and Eigenmann, 1889a
	Psectrogaster amazonica Eigenmann and Eigenmann, 1889a
	Curimatus falcatus Eigenmann and Eigenmann, 1889b
	Curimatus isognathus Eigenmann and Eigenmann, 1889b
	Psectrogaster auratus Gill, 1895
	Psectrogaster curviventris Eigenmann and Kennedy, 1903
	Curimata pearsoni Myers, 1929
	Curimata saguiru Fowler, 1941
	Psectrogaster rhomboides australe Risso and Sanchez, 1964
Steindachnerina	*Curimatus argenteus* Gill, 1858
	Curimatus leuciscus Günther, 1868
	Curimatus dobula Günther, 1868
	Curimatus elegans Steindachner, 1874
	Curimatus bimaculatus Steindachner, 1876
	Curimatus trachystetus Cope, 1878
	Curimatus nasus Steindachner, 1882b
	Curimatus hypostoma Boulenger, 1887
	Curimatus bimaculatus sialis Eigenmann and Eigenmann, 1889b
	Curimatus elegans bahiensis Eigenmann and Eigenmann, 1889b
	Curimatus gilberti brevipinnis Eigenmann and Eigenmann, 1889b
	Curimatus guntheri Eigenmann and Eigenmann, 1889b
	Curimatus conspersus Holmberg, 1891
	Curimatus nitens Holmberg, 1891
	Curimatus nigrotaenia Boulenger, 1902
	Curimatus leuciscus bolivae Eigenmann and Ogle, 1907
	Prochilodus stigmaturus Fowler, 1911
	Curimatus elegans var. *amazonica* Steindachner, 1911
	Curimatus atratoensis Eigenmann, 1912b
	Curimatus issororoensis Eigenmann, 1912a
	Curimatus morawhannae Eigenmann, 1912a
	Prochilodus pterostigma Fowler, 1913b
	Curimatus semiornatus Steindachner, 1914
	Curimatus metae Eigenmann, 1922
	Curimatus binotatus Pearson, 1924
	Curimatus notonotus Miranda Ribeiro, 1937
	Curimata melaniris Fowler, 1940
	Curimata hypostoma hastata Allen, 1942 (in Eigenmann and Allen, 1942)
	Curimatus robustula Allen, 1942 (in Eigenmann and Allen, 1942)
	Curimata niceforoi Fowler, 1943
	Allenina pectinata Fernández-Yépez, 1948
	Cruxentina insculpta Fernández-Yépez, 1948
	Curimata fasciata Vari and Géry, 1985
	Curimata stigmosa Vari, 1987
	Curimata biornata, Braga and Azpelicueta, 1987
Pseudocurimata	*Anodus troschelii* Günther, 1859
	Curimatus boulengeri Eigenmann, 1907 (in Eigenmann and Ogle, 1907)
	Curimatus brevipes Eigenmann and Ogle, 1907
	Curimatus aureus Pellegrin, 1908
	Curimatus lineopunctatus Boulenger, 1911
	Curimatus patiae Eigenmann, 1914 (in Eigenmann, Henn, and Wilson, 1914)
	Curimatus peruanus Eigenmann, 1922
Curimatella	*Anodus alburnus* Müller and Troschel, 1845
	Curimatus Meyeri Steindachner, 1882b
	Curimatus dorsalis Eigenmann and Eigenmann, 1889b
	Curimatus lepidurus Eigenmann and Eigenmann, 1889a
	Curimatus leucostictus Eigenmann and Eigenmann, 1889b

TABLE 2.—Continued.

Recognized genus	Included species
	Curimatus serpae Eigenmann and Eigenmann, 1889a
	Curimatus alburnus australe Eigenmann and Kennedy, 1903
	Curimatus elegans paraguayensis Eigenmann and Kennedy, 1903
	Curimatus (Curimatella) xinguensis Steindachner, 1908
	Curimatus (Curimatella) alburnus var. *caudimaculata* Pellegrin, 1909
	Curimatus bolivarensis Steindachner, 1910
	Curimata reticulata Allen, 1942 (in Eigenmann and Allen, 1942)
	Lepipinna immaculata Fernández-Yépez, 1948
Cyphocharax	*Curimata Gilbert* Quoy and Gaimard, 1824
	Curimatus abramoides Kner, 1859
	Curimatus spilurus Günther, 1864
	Curimatus voga Hensel, 1869
	Curimatus albula Lütken, 1874
	Curimatus Magdalenae Steindachner, 1879
	Curimatus platanus Günther, 1880
	Curimatus Nagelii Steindachner, 1882a
	Curimatus microcephalus Eigenmann and Eigenmann, 1889b
	Curimatus plumbeus Eigenmann and Eigenmann, 1889b
	Curimatus spiluropsis Eigenmann and Eigenmann, 1889b
	Curimatus gillii Eigenmann and Kennedy, 1903
	Curimatus notatus Steindachner, 1908
	Curimatus helleri Steindachner, 1910
	Curimatus surinamensis Steindachner, 1910
	Curimatus stigmaturus Fowler, 1913b
	Curimatus multilineatus Myers, 1927
	Curimata esperanze Myers, 1929
	Curimatus hermanni Ahl, 1931
	Curimatella rehni Fowler, 1932
	Curimatopsis saladensis Meinken, 1933
	Curimatopsis maculatus Ahl, 1934
	Curimatoides ucayalensis Fowler, 1940
	Curimatus Vandeli Puyo, 1943
	Pseudocurimata grandocule Fernández-Yépez, 1948
	Curimatorbis modestus Fernández-Yépez, 1948
	Pseudocurimata santacatarinae Fernández-Yépez, 1948
	Pseudocurimata steindachneri Fernández-Yépez, 1948
	Curimatus (Hemicurimata) esperanzae pijpersi Géry, 1965
	Curimata vanderi Britski, 1980
	Curimata punctata Vari and Nijssen, 1986
	Curimata spilota Vari, 1987

TABLE 3.—Nominal species within the Curimatidae, their describers and date of description, together with the genera to which they are assigned in this study. Species are arranged alphabetically by specific, subspecific, or varietal epithet, and are cited as in their original description. Undescribed species (e.g., species A, B) are not included.

Species, author, and date of description	Genus
Curimatus abramoides Kner, 1859	*Cyphocharax*
Curimatus albula Lütken, 1874	*Cyphocharax*
Anodus alburnus Müller and Troschel, 1845	*Curimatella*
Lambepiedra alleni Fernández-Yépez, 1948	*Curimata*
Curimatus altamazonicus Cope, 1878	*Potamorhina*
Psectrogaster amazonica Eigenmann and Eigenmann, 1889a	*Psectrogaster*
Curimatus elegans var. *amazonica* Steindachner, 1911	*Steindachnerina*
Curimatus argenteus Gill, 1858	*Steindachnerina*
Curimatus asper Günther, 1868	*Curimata*
Curimatus atratoensis Eigenmann, 1912b	*Steindachnerina*
Psectrogaster auratus Gill, 1895	*Psectrogaster*
Curimatus aureus Pellegrin, 1908	*Pseudocurimata*
Curimatella alburnus australe Eigenmann and Kennedy, 1903	*Curimatella*
Psectrogaster rhomboides australe Risso and Sanchez, 1964	*Psectrogaster*
Curimatus elegans bahiensis Eigenmann and Eigenmann, 1889b	*Steindachnerina*
Curimatus bimaculatus Steindachner, 1876	*Steindachnerina*
Curimatus binotatus Pearson, 1924	*Steindachnerina*
Curimata biornata Braga and Azpelicueta, 1987	*Steindachnerina*
Curimatus leuciscus bolivae Eigenmann and Ogle, 1907	*Steindachnerina*
Curimatus bolivarensis Steindachner, 1910	*Curimatella*
Curimatus boulengeri Eigenmann, 1907 (in Eigenmann and Ogle, 1907)	*Pseudocurimata*
Curimatus brevipes Eigenmann and Ogle, 1907	*Pseudocurimata*
Curimatus gilberti brevipinnis Eigenmann and Eigenmann, 1889b	*Steindachnerina*
Curimatus alburnus var. *caudimaculatus* Pellegrin, 1909	*Curimatella*
Curimata cerasina Vari, 1984b	*Curimata*
Anodus ciliatus Müller and Troschel, 1845	*Psectrogaster*
Psectrogaster cisandina Allen, 1942 (in Eigenmann and Allen, 1942)	*Curimata*
Curimatus conspersus Holmberg, 1891	*Steindachnerina*
Curimata copei Fowler, 1906	*Curimata*
Curimatopsis crypticus Vari, 1982a	*Curimatopsis*
Psectrogaster curviventris Eigenmann and Kennedy, 1903	*Psectrogaster*
Salmo cyprinoides Linnaeus, 1766	*Curimata*
Curimatus dobula Günther, 1868	*Steindachnerina*
Curimatus dorsalis Eigenmann and Eigenmann, 1889b	*Curimatella*
Salmo edentulus Bloch, 1794	*Curimata*
Curimatus elegans Steindachner, 1874	*Steindachnerina*
Curimata esperanzae Myers, 1929	*Cyphocharax*
Curimatus essequibensis Günther, 1864	*Psectrogaster*
Curimatopsis evelynae Géry, 1964a	*Curimatopsis*
Curimatus falcatus Eigenmann and Eigenmann, 1889b	*Psectrogaster*

TABLE 3.—Continued.

Species, author, and date of description	Genus
Curimata fasciata Vari and Géry, 1985	*Steindachnerina*
Curimata Gilbert Quoy and Gaimard, 1824	*Cyphocharax*
Curimatus gillii Eigenmann and Kennedy, 1903	*Cyphocharax*
Pseudocurimata grandocule Fernández-Yépez, 1948	*Cyphocharax*
Curimatus guntheri Eigenmann and Eigenmann, 1889b	*Steindachnerina*
Curimata hypostoma hastata Allen, 1942 (in Eigenmann and Allen, 1942)	*Steindachnerina*
Curimatus helleri Steindachner, 1910	*Cyphocharax*
Curimatus hermanni Ahl, 1931	*Cyphocharax*
Curimatus hypostoma Boulenger, 1887	*Steindachnerina*
Lepipinna immaculata Fernández-Yépez, 1948	*Curimatella*
Salmo immaculatus Linnaeus, 1758	*Curimata*
Curimata incompta Vari, 1984b	*Curimata*
Cruxentina insculpta Fernández-Yépez, 1948	*Steindachnerina*
Curimatus isognathus Eigenmann and Eigenmann, 1889b	*Psectrogaster*
Curimatus issororoensis Eigenmann, 1912a	*Steindachnerina*
Curimatus knerii Steindachner, 1876	*Curimata*
Curimatus laticeps Valenciennes, 1849 (in Cuvier and Valencinnes, 1849)	*Potamorhina*
Anodus latior Spix, 1829 (in Spix and Agassiz, 1829)	*Potamorhina*
Curimatus lepidurus Eigenmann and Eigenmann, 1889a	*Curimatella*
Curimatus leuciscus Günther, 1868a	*Steindachnerina*
Curimatus leucostictus Eigenmann and Eigenmann, 1889b	*Curimatella*
Curimatus lineopunctatus Boulenger, 1911	*Pseudocurimata*
Curimatopsis macrocephalus Ahl, 1931	*Curimatopsis*
Curimata (Curimatopsis) macrolepis Steindachner, 1876	*Curimatopsis*
Curimatus macrops Eigenmann and Eigenmann, 1889b	*Curimata*
Curimatopsis maculatus Ahl, 1934	*Cyphocharax*
Curimatus Magdalenae Steindachner, 1879	*Cyphocharax*
Curimata melanira Fowler, 1940	*Steindachnerina*
Curimatus metae Eigenmann, 1922	*Steindachnerina*
Curimatus Meyeri Steindachner, 1882b	*Curimatella*
Curimatus microcephalus Eigenmann and Eigenmann, 1889b	*Cyphocharax*
Curimatopsis microlepis Eigenmann and Eigenmann, 1889a	*Curimatopsis*
Curimatus mivartii Steindachner, 1878	*Curimata*
Curimatorbis modestus Fernández-Yépez, 1948	*Cyphocharax*
Curimatus morawhannae Eigenmann, 1912a	*Steindachnerina*
Curimatus multilineatus Myers, 1927	*Cyphocharax*
Curimata murieli Allen, 1942 (in Eigenmann and Allen, 1942)	*Curimata*
Curimatopsis myersi Vari, 1982b	*Curimatopsis*
Curimatus Nagelii Steindachner, 1882a	*Cyphocharax*
Curimatus nasus Steindachner, 1882b	*Steindachnerina*
Curimata niceforoi Fowler, 1943	*Steindachnerina*
Curimatus nigrotaenia Boulenger, 1902	*Steindachnerina*
Curimatus nitens Holmberg, 1891	*Steindachnerina*
Curimatus notatus Steindachner, 1908	*Cyphocharax*
Curimatus nototonotus Miranda-Ribiero, 1937	*Steindachnerina*
Curimatus ocellatus Eigenmann and Eigenmann, 1889b	*Curimata*
Curimatus elegans paraguayensis Eigenmann and Kennedy, 1903	*Curimatella*
Curimatus patiae Eigenmann, 1914 (in Eigenmann, Henn, and Wilson, 1914)	*Pseudocurimata*
Curimata pearsoni Myers, 1929	*Psectrogaster*
Allenina pectinata Fernández-Yépez, 1948	*Steindachnerina*
Curimatus peruanus Eigenmann, 1922	*Pseudocurimata*
Curimatus (Hemicurimata) esperanzae pijpersi Géry, 1965	*Cyphocharax*
Charax planirostris Gray, 1854	*Curimata*
Curimatus platanus Günther, 1880	*Cyphocharax*
Curimatus plumbeus Eigenmann and Eigenmann, 1889b	*Cyphocharax*
Curimatus (Anodus) pristigaster Steindachner, 1876	*Potamorhina*
Prochilodus pterostigma Fowler, 1913b	*Steindachnerina*
Curimata punctata Vari and Nijssen, 1986	*Cyphocharax*
Curimatella rehni Fowler, 1932	*Cyphocharax*
Curimata reticulata Allen, 1942 (in Eigenmann and Allen, 1942)	*Curimatella*
Psectrogaster rhomboides Eigenmann and Eigenmann, 1889a	*Psectrogaster*
Curimata robustula Allen, 1942 (in Eigenmann and Allen, 1942)	*Steindachnerina*
Curimatus rutiloides Kner, 1859	*Psectrogaster*
Curimata saguiru Fowler, 1941	*Psectrogaster*
Curimatopsis saladensis Meinken, 1933	*Cyphocharax*
Pseudocurimata santacatarinae Fernández-Yépez, 1948	*Cyphocharax*
Curimatus schomburgkii Günther, 1864	*Curimata*
Curimatus semiornatus Steindachner, 1914	*Steindachnerina*
Curimatus semitaeniatus Steindachner, 1917	*Curimata*
Curimatus serpae Eigenmann and Eigenmann, 1889a	*Curimatella*
Curimatus bimaculatus sialis Eigenmann and Eigenmann, 1889b	*Steindachnerina*
Curimatus simulatus Eigenmann and Eigenmann, 1889b	*Curimata*
Curimata spilota Vari, 1987	*Cyphocharax*
Curimatus spiluropsis Eigenmann and Eigenmann, 1889b	*Cyphocharax*
Curimatus spilurus Günther, 1864	*Cyphocharax*
Semitapiscis squamoralevis Braga and Azpelicueta, 1983	*Potamorhina*
Pseudocurimata steindachneri Fernández-Yépez, 1948	*Cyphocharax*
Curimata stigmosa Vari, 1987	*Steindachnerina*
Prochilodus stigmaturus Fowler, 1911	*Steindachnerina*
Curimatus stigmaturus Fowler, 1913a	*Cyphocharax*
Curimatus surinamensis Steindachner, 1910	*Cyphocharax*
Curimatus trachystetus Cope 1878	*Steindachnerina*
Anodus troschelii Günther, 1859	*Pseudocurimata*
Curimatoides ucayalensis Fowler, 1940	*Cyphocharax*
Curimatus Vandeli Puyo, 1943	*Cyphocharax*
Curimatus vanderi Britski, 1980	*Cyphocharax*
Curimatus vittatus Kner, 1859	*Curimata*
Curimatus voga Hensel, 1869	*Cyphocharax*
Curimatus (Curimatella) xinguensis Steindachner, 1908	*Curimatella*

NOTE: *Curimatus alberti* cited by Günther (1880) and Eigenmann and Eigenmann (1889b) is presumably a lapsus for *Cypocharax gilberti* (Quoy and Gaimard, 1824). *Curimatus hasemanni* referred to by Fernández-Yépez (1948:73) is evidently an incorrect citation of *Curimatus hermanni* Ahl (1931). As noted by Géry (1972:33), *Curimatus tigris* Fowler (1913a) is actually a member of the Prochilodontidae. Vari and Castro (1988) demonstrate that *Prochilodus stigmaturus* Fowler (1911) is a species of *Steindachnerina*.

MATERIAL EXAMINED.—Osteological and myological materials examined are deposited in the following museums: Museo de Biologia, Universidad Central de Venezuela, Caracas (MBUCV); the Museum of Comparative Zoology, Harvard University, Cambridge (MCZ); the Museo de Zoologia da Universidade de São Paulo (MZUSP); and the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

The following specimens are the basis for text illustrations or specific observations noted in the text. Measurements, in mm, are of standard length (SL).

ANOSTOMIDAE

Abramites hypselonotus (Günther), USNM 164036; 1 specimen, 100.5 mm; Ecuador, lower Río Bobonaza.

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 locality data.

Gnathodolus bidens Myers, USNM 231539; 1 specimen, 76.2 mm; aquarium material.

Laemolyta species, USNM 179514; 2 specimens, 75.3–77.0 mm; Brazil, Amazonas, Rio Urubu.

Leporellus vittatus Valenciennes, USNM uncatalogued, 1 specimen, 121.4 mm; Venezuela, Barinas, Río Las Palmas.

Rhytiodus microlepis Kner, USNM 163850; 1 specimen, 131.7 mm; Peru, Loreto, Iquitos.

Schizodon fasciatum Agassiz, USNM 179507; 1 specimen, 49.3 mm; Brazil, Amazonas, Rio Urubu.

Synaptolaemus cingulatus Myers and Fernández-Yépez, MBUCV V-4252; 1 specimen, 71.2 mm; Venezuela, Río Paragua.

CHARACIDAE

Agoniates species, USNM 243222; 1 specimen, 65.6 mm; Brazil, Amazonas, mouth of Rio Içа.

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

Alestes longipinnis (Günther), USNM 285665; 3 specimens, 44.7–50.5 mm; Togo, Togble-Kope.

Brycon falcatus Müller and Troschel, USNM 226161; 2 specimens, 71.3–78.3 mm; Surinam, Nickerie District, Corantijn River (Figures 6, 18).

Cataprion mento Müller and Troschel, USNM 257547; 1 specimen, 55.2 mm; Venezuela, Estado Apure, Río Cunaviche.

Clupeacharax anchovoides Pearson, USNM 243223; 2 specimens; 57.6–58.7 mm; Peru, Ucayali, Pucallpa.

Exodon paradoxus Müller and Troschel, USNM uncatalogued; 1 specimen, 69.3 mm; Brazil, Goiás, Rio Tocantins.

Hollandichthys sp., USNM 285668; 3 specimens, 53.5–71.8 mm; no locality data.

Hydrocynus species, USNM 285669; 3 specimens, 38.5–59.2 mm; Volta [Ghana], Black Volta River.

Lepidarchus adonis Roberts, USNM 267290; 5 specimens, 16.8–21.3 mm; Ghana, Aluku.

Phenacogrammus pabrensis Roman, USNM 285666; 2 specimens, 31.0–33.7 mm; Ghana, Dayi River at Vakpo.

CHILODONTIDAE

Caenotropus labyrinthicus (Kner), USNM 231544; 1 specimen. 64.2 mm; Venezuela, Territorio Federal Amazonas, upper Río Orinoco at Tama Tama.

Caenotropus labyrinthicus (Kner), USNM 231543; 1 specimen, 58.5 mm; Brazil, Amazonas, Rio Negro.

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

Chilodus punctatus Müller and Troschel, USNM 231542, 13 specimens, 27.1–38.2 mm; Peru, Loreto, Río Nanay.

CITHARINIDAE

Citharinus citharus Geoffroy, USNM 52146; 1 specimen, 218.7 mm; Egypt, Nile River.

CURIMATIDAE

Cyphocharax abramoides (Kner), USNM 267952, 1 specimen, 110.3 mm; Brazil, Pará, Rio Xingu, Belo Monte (Figures 2, 32).

Cyphocharax helleri (Steindachner), USNM 220158; 3 specimens, 48.7–66.3 mm; Surinam, Brokopondo District, Gran Kreek, 63 km from Afobaka.

Cyphocharax magdalenae (Steindachner), USNM 220197; 2 specimens, 78.7–112.3; Panama, Chiriqui, creek 3 mi [4.8 km] W of San Juan on Inter-American Highway.

Cyphocharax microcephala (Eigenmann and Eigenmann), USNM 225307; 2 specimens, 28.7–49.3 mm; Surinam, Nickerie Distict, Kapoeri Creek.

Curimata cisandina (Allen), USNM 229171, 1 specimen, 89.9 mm; Brazil, Amazonas, Rio Solimões, Paraná da Ilha Marchantaria (Figure 19).

Curimata cyprinoides (Linnaeus), USNM 231433; 2 specimens, 17.1–21.4 mm; Surinam, Nickerie District, Corantijn River (Figure 7).

Curimata cyprinoides (Linnaeus), USNM 267964; 1 specimen, 115 mm; Brazil, Amapa, Rio Araguari, Ferreira Gomes (Figures 8, 22, 23, 26C, 27C, 36C, 42D).

Curimata cyprinoides (Linnaeus), USNM 225619; 1 specimen, 79.2 mm; Surinam, Nickerie District, Makilikabroe Creek (Figure 14).

Curimata cyprinoides (Linnaeus), USNM 267963; 2 specimens, 110.5–125.0 mm; Brazil, Pará, Rio Xingu, Belo Monte (Figures 28, 30).

Curimata incompta Vari, USNM 273308; 1 specimen, 81.2 mm; Venezuela, Estado Bolivar, small isolated caño normally draining into Río Orinoco, downstream of El Burro (Figure 3).

Curimata ocellata Eigenmann and Eigenmann, USNM 267973; 1 specimen, 160.3 mm; Brazil, Amazonas, Rio Marauia (Figure 1).

Curimatella alburna (Müller and Troschel), MZUSP 6309; 1 specimen, 98.3 mm; Brazil, Amazonas, mouth of Rio Purus, Lago Castro (Figures 13, 39).

Curimatella meyeri (Steindachner), USNM 261508; 1 specimen, 100.1 mm; Peru, Ucayali, Río Ucayali, Masisea (Figure 35C).

Curimatopsis microlepis Eigenmann and Eigenmann, MZUSP 21053; 1 specimen, 96.0 mm; Brazil, Amazonas, Rio Negro (Figures 5, 15).

Curimatopsis microlepis Eigenmann and Eigenmann, USNM 268867; 1 specimen, 75.8 mm; Brazil, Amazonas, Rio Solimões near Beruri (Figures 12, 22A, 26, 27B, 38A, 39, 40A, 42).

Potamorhina altamazonica (Cope), USNM 257367; 1 specimen, 119.8 mm; Peru, Loreto, Río Amazonas, near Iquitos (Figures 33A, 35B, 36B, 42B).

Potamorhina laticeps (Valenciennes), USNM 121325; 1 specimen, 129.3 mm; Venezuela, Zulia, Lago Maracaibo basin (Figures 10, 22B, 41A).

Potamorhina squamoralevis (Braga and Azpelicueta), USNM 243228; 1 specimen, 90.2 mm; Brazil, Mato Grosso, Baia do Buritizal (Figures 21, 25).

Psectrogaster amazonica Eigenmann and Eigenmann, USNM 261518, 1 specimen, 106.0 mm; Peru, Ucayali, Río Ucayali, Pucallpa (Figures 22C, 36A).

Psectrogaster ciliata (Muüller and Troschel), USNM 269990; 1 specimen, 94.8 mm; Venezuela, Estado Bolivar, small isolated caño normally draining into Río Orinoco, downstream of El Burro (Figures 26B, 38B, 41B, 42C).

Psectrogaster curviventris Eigenmann and Kennedy, USNM 243221; 1 specimen, 72.9 mm; Brazil, Mato Grosso, Baia do Buritizal (Figures 9, 35A).

Pseudocurimata boulengeri (Eigenmann), USNM 285671; 4 specimens, 83.4–92.7 mm; Ecuador, Vinces.

Pseudocurimata lineopunctata (Boulenger), MCZ 54029; 1 specimen, 78.1

mm; Ecuador, Esmeraldas, Estero La Boveda, 4 km from Camerones (Athahualpa).

Pseudocurimata patiae (Eigenmann), USNM 285672; 1 specimen, 82.1 mm; Colombia, Rio Patia, Barbacoas.

Pseudocurimata peruanus (Eigenmann), USNM 285667; 1 specimen, 90.5 mm; Peru, Piura, Tinajones (Figure 43C).

Pseudocurimata troscheli Günther, USNM 285673; 1 specimen, 80.5 mm; Ecuador, Colimes.

Steindachnerina argentea (Gill), USNM 285663; 1 specimen, 83.5 mm; Trinidad, northern Trinidad, Arouca River, just north of Churchill-Roosevelt Highway (Figure 40B).

Steindachnerina bimaculata (Steindachner), USNM 251450; 2 specimens, 61.5–75.4 mm; Peru, Loreto, Río Amazonas, opposite Tabatinga, Brazil (Figures 33B, 34B, 37).

Steindachnerina conspersa (Holmberg), USNM 232224; 1 specimen, 83.2 mm; Paraguay, Presidente Hayes, off Trans-Chaco Highway at km 50 (Figure 36D).

Steindachnerina hypostoma (Boulenger), USNM 167802; 1 specimen, 82.7 mm; Peru, Río Huallaga (Figures 11, 20, 24).

Steindachnerina hypostoma (Boulenger), USNM 261493; 1 specimen, 76.8 mm; Peru, Ucayali, Pucallpa (Figure 29).

Steindachnerina hypostoma (Boulenger), USNM 261513; 1 specimen, 73.4 mm; Peru, Ucayali, Río Ucayali, Pucallpa (Figure 31).

DISTICHODONTIDAE

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

Nannocharax intermedius Boulenger, USNM 231555; 2 specimens, 50.7–63.4 mm; West Africa.

Paradistichodus dimidiatus Pellegrin, USNM 231556; 2 specimens, 45.6–47.3 mm; Ghana, Dayi River.

Xenocharax spilurus Günther, USNM 227693; 1 specimen, 89.3 mm; Gabon, Lac Ezanga (Figure 4).

HEMIODONTIDAE

Anodus elongatus Spix, USNM 231550; 1 specimen, 120.3 mm; Peru, Loreto, Río Ucayali.

Argonectes scapularis Böhlke and Myers, USNM 243224; 1 specimen, 125.4 mm; Brazil, Amazonas, Río Janauperi.

Bivibranchia bimaculata Vari, USNM 225974; 1 specimen, 97.0 mm; Surinam, Nickerie District, Corantijn River.

Bivibranchia protractila Eigenmann, USNM 194363; 1 specimen, 62.8 mm; Brazil, Mato Grosso, upper Rio Juruena.

Hemiodopsis ocellata Vari, USNM 225593; 1 specimen, 99.6 mm; Surinam, Nickerie District, 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.

HEPSETIDAE

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

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.

PROCHILODONTIDAE

Ichthyoelephas species, USNM 231437; 1 specimen, 110.2 mm; Ecuador.

Prochilodus nigricans Agassiz, USNM 231438; 1 specimen, 144.3 mm; Bolivia, Tumpasa (Figures 6, 16).

Prochilodus rubrotaeniatus Schomburgk, USNM 225419; 1 specimen, 108.7 mm; Surinam, Nickerie District, Corantijn River (Figure 27A).

Semaprochilodus laticeps Steindachner, USNM 270239; 1 specimen, 68.5 mm SL; Venezuela, Estado Bolivar, caño off Río Orinoco at El Burro (Figure 34A).

In addition to the listed specimens, a large number of dry skeletons, stained and cleared glycerine preparations, and alcohol preserved specimens of nearly all species of the family Curimatidae were examined in the comparative studies associated with the present analysis. The majority of those collections are deposited in the collections of the AMNH, MBUCV, MZUSP, and USNM, with lesser numbers of specimens being from the holdings of the other institutions noted under "Acknowledgments."

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

AA	angulo-articular
AC	anterior ceratohyal
AD	anterodorsal laterosensory canal segment of sixth infraorbital (IO$_6$)
AE	anterior extension of ventral process of third hypobranchial (H$_3$)
AI	area of insertion of ligamentum primordiale
ALP	anterior lobulate processes of buccopharyngeal complex
AS	anterior spur of fourth epibranchial (E$_4$)
ASE$_3$	anterior articular surface of third epibranchial (E$_3$)
ASMQF	anterior section of metapterygoid-quadrate fenestra
AVPE$_4$	anteroventral portion of fourth epibranchial (E$_4$)
BB	basibranchial (1 to 4)
BC	buccopharyngeal complex
BH	basihyal
BHC	basihyal cartilage
BHTP	basihyal tooth plate
BR	branchiostegal rays (1 to 4)
C	ceratobranchial (1 to 5)
CART	cartilage
CB-LP	cartilage body of ligamentum primordiale
CCH$_3$	common posterior cartilage of third hypobranchials (H$_3$)
DCE	distal cartilage of epibranchial (3 or 4)
DEN	dentary
DFPB$_3$	dorsal flange of third infrapharyngobranchial (PB$_3$)
DH	dorsal hypophyal
DLF	dorsolateral flange of second infrapharyngobranchial (PB$_2$)
E	epibranchial (1 to 5)
ECT	ectopterygoid
EPC	ethmopalatine cartilage
FP	first proximal radial pterygiophore of dorsal fin
GA	gill arch
H	hypobranchial (1 to 3)
HC-IO$_4$	horizontal laterosensory canal of fourth infraorbital (IO$_4$)
HY	hyomandibula
IL	insertion point of ligament between second and third hypobranchials (H$_2$ and H$_3$)
IO	infraorbital (1 to 6)
LF	lateral fold of buccopharyngeal complex
LIG	ligament
LP	ligamentum primordiale

LPE$_3$	lateral articular process of third epibranchial (E$_3$)
LR	lateral ridge on dorsal surface of fourth ceratobranchial (C$_4$)
MBS	medial bony spur of fourth epibranchial (E$_4$)
MES	mesopterygoid
MET	metapterygoid
METR	metapterygoid ridge
MF	median fleshy fold of buccopharyngeal complex
MPE$_3$	medial articular process of third epibranchial (E$_3$)
MPL	mucous producing layer of buccopharyngeal complex
MQF	metapterygoid-quadrate fenestra
MR	medial ridge on dorsal surface of fourth ceratobranchial (C$_4$)
MVL	mid-ventral ligament
MX	maxilla
N	notch of premaxilla receiving rear portion of premaxilla
NS	neural spines (1 to 7)
PAL	palatine
PB	infrapharyngobranchial (1 to 4)
PC	posterior ceratohyal
PD	posterodorsal laterosensory canal segment of sixth infraorbital (IO$_6$)
PDAS	posterodorsal articular surface of palatine
PE	posterior extension of ventral process of third hypobranchial (H$_3$)
PLP	posterior lobulate process of buccopharyngeal complex
PMX	premaxilla
POP	preopercle
PP	posterior process of maxilla
PSMQF	posterior section of metapterygoid-quadrate fenestra
QU	quadrate
RA	retroarticular
SF	secondary fleshy folds of buccopharyngeal complex
SN	supraneurals (1 to 6)
SPH	sphenotic
SUOP	supraopercle
SYM	symplectic
TCBB$_3$	terminal cartilage of third basibranchial (BB$_3$)
UL	upper lip
UN	uncinate process
UP	upper pharyngeal tooth plate (4 or 5)
VAP	ventral articular process of fourth epibranchial (E$_4$)
VH	ventral hypohyal
VLF	ventrolateral flange of second infrapharyngobranchial (PB$_2$)
VPE$_4$	ventral plate of fourth epibranchial (E$_4$)
VPH$_3$	ventral process of third hypobranchial (H$_3$)

Character Description and Analysis

The primary focus of the present study is the advancement of an explicit hypothesis of the phylogenetic relationships within the Curimatidae. Characters that were discovered to demonstrate phylogenetically significant variation are discussed in this section, along with their taxonomic distributions and the information from outgroup and ontogenetic studies that permits their polarization.

The evidence from the different analyzed characters is brought together under "Synapomorphy List and Phylogenetic Reconstruction" to advance the most parsimonious hypothesis of phylogenetic relationships within the Curimatidae. That hypothesis will, in turn, be used as the basis to evaluate the utility of previous intrafamilial classifications as indicators of the phylogenetic history of the subunits of the family. Since the aim of the present study is the derivation of an hypothesis of the evolutionary history within the Curimatidae, I will not present a detailed description of the osteology and soft anatomy of the involved lineages. Only anatomical systems that show variation relevant to the intrafamilial phylogenetic reconstruction are discussed.

In a few instances, characters pertinent to the question of the monophyly of the lineage formed by the Curimatidae and Prochilodontidae, or relevant to hypotheses proposed in previous studies (Vari, 1982a, 1983, 1984a) are also discussed. Character variation at levels less inclusive than the genus is not usually detailed. Exceptions involve the genera *Curimatopsis* and *Potamorhina* which have already been revised (Vari, 1982a and 1984a, respectively) and which were the subjects of associated phylogenetic analyses. Species level relationships within the remaining groups will be analyzed as part of forthcoming revisionary studies.

Among the hypothesized derived characters discovered during this study, some were found to have distributions within the Curimatidae incongruent with the most parsimonious hypothesis of relationships based on the overall distribution of all synapomorphies. Such homoplasies are not recognizable a priori, but can only be identified within the context of the final phylogenetic hypothesis. Homoplasious characters and the degree to which different groups of characters contribute to the final sets of congruent synapomorphies and homoplasies is analyzed in the section "Convergent Characters." Nonetheless, in order to simplify the discussion, homoplasies and their distributional incongruities relative to the hypothesized phylogeny will also be discussed at appropriate points in this section.

BRANCHIAL ARCHES

The bones, cartilages, and associated connective tissues and muscles of the branchial arches have been a source of considerable morphological information pertinent to the elucidation of the phylogenetic relationships of the Curimatidae. The eight derived branchial basket characters listed by Vari (1983:11–24, 47) for the Curimatidae and Prochilodontidae represent the majority of the hypothesized synapomorphies for that clade. Similarly, half of the characters uniting the lineage consisting of the Curimatidae and Prochilodontidae to the clade formed by the Anostomidae and Chilodontidae are gill arch synapomorphies (Vari, 1983:46–47). Research associated with this study has uncovered an additional derived modification in the dorsal portions of the branchial basket whose phyletic distribution is congruent with a hypothesis of a sister group relationship between the Curimatidae and Prochilodontidae along with three additional synapomorphies for the species of the Curimatidae. This system also demonstrates numerous characters that are informative relative to a hypothesis of generic level relationships within the Curimatidae.

Dorsal Portion of Branchial Arches

The large number of synapomorphies in the bones, cartilages, and ligaments of the dorsal portions of the branchial system within the Curimatidae are discussed below. In order to simplify discussion of the numerous characters found in the multitude of individual elements in that system, the analysis is arranged around subunits of the arches. These subunits typically consist of individual components (e.g., the fourth epibranchial and its associated cartilages and ligaments), although in some situations, functional complexes (e.g., the dorsal portion of a single branchial arch) will be the unit of analysis.

The branchial arches of prochilodontids, the hypothesized sister group to the Curimatidae (Vari, 1983), serve as the best available approximation of the plesiomorphous condition of most components of the branchial system for curimatids. Prochilodontids demonstrate derived gill arch modifications hypothesized as common to the presumed ancestor of that family and the Curimatidae. Apart from those few derived modifications unique to the family, the prochilodontid branchial basket retains overall its hypothesized ancestral condition. The Prochilodontidae demonstrates only one modification of the condition of the upper portion of the gill arches hypothesized as common to the ancestors of prochilodontids and curimatids that is significant for the following discussion. That character involves the form of the fifth upper pharyngeal tooth plate (UP_5). All members of the Prochilodontidae have that element restructured into a vertically expanded, transversely flattened plate, an alteration unique for the members of that family among Characiformes (Vari, 1983:19, 49; Figure 6).

As a consequence of its apomorphous nature, the UP_5 of the Prochilodontidae cannot serve as an approximation of the plesiomorphous condition of that element for comparative studies within the Curimatidae. Rather it is necessary to use more distant outgroups in polarizing character state transition series for that ossification. The sister group to the Prochilodontidae and Curimatidae, the clade formed by the Anostomidae and Chilodontidae, also has the fifth upper pharyngeal tooth plate significantly altered autapomorphously (Vari, 1983:19), making the condition of UP_5 in that lineage similarly inappropriate as an approximation of the plesiomorphous state of the bone in curimatids. Rather it is necessary to refer to phyletically more distant characiform taxa as outgroups. The absence of a definitive hypothesis of a sister group to the lineage formed by the four families (Curimatidae, Prochilodontidae, Anostomidae, and Chilodontidae) obscures the exact outgroup most appropriate for outgroup comparisons to that clade. This ambiguity necessitates reference to all other characiforms as a general outgroup for comparisons involving UP_5.

Fourth and Fifth Epibranchials (E_4, E_5)

Vari (1983:48) listed ten synapomorphies for the members of the Curimatidae (see also "Synapomorphy List and Phylogenetic Reconstruction"). An eleventh shared derived character involving the ventral margin of the fourth epibranchial of curimatids has been found in the morphological studies aimed at deriving a hypothesis of phylogenetic relationships within the family, herein. The anteroventral portion of the fourth epibranchial ($AVPE_4$, Figure 4) in characiform outgroups extends more ventrally than the remainder of the bone and forms a discrete anteroventral process of the element. That enlarged anterior portion of the bone has two major articular facets. The broad anterior articular surface contacts the posterior portion of the fourth infrapharyngobranchial (PB_4), and the smaller ventral articular surface serves as the region of attachment for the fifth upper pharyngeal tooth plate (UP_5) (e.g., *Xenocharax spilurus*, Figure 4). The main body of E_4 lies posterior and dorsal of this anteroventral articular portion of the bone, with the two sections of E_4 relatively discrete. The main body of the fourth epibranchial has a transversely rounded ventral margin that is somewhat thickened relative to the plate-like triangular portion of the bone that extends dorsal of it. In curimatids the anteroventral articular portion of the fourth epibranchial and this posterior horizontal ventrally rounded section of the bone are not as discrete as in the outgroups. This fusion, an apomorphous conditon, is the consequence of the presence of an additional transversely flattened vertical plate of bone along the ventral portion of the main body of E_4 (SYNAPOMORPHY 26). That plate (VPE_4) extends along the ventral margin of the main body of E_4 from the posterior surface of the anteroventral articular process of the bone ($AVPE_4$) (Figure 5). This plate is horizontally elongate overall with a somewhat triangular shape. It is most developed anteriorly where it is continuous along a vertical line with the posterior surface of the articular process of UP_5. The height of the bony plate gradually tapers posteriorly, with the exact form and orientation of the plate in different curimatids a function of the overall morphology of the fourth epibranchial in those lineages.

The main body of the fourth epibranchial also demonstrates a notable degree of phylogenetically informative variability within the Curimatidae. The generalized plan of the bone among prochilodontids serves well as an example of the outgroup condition for the Curimatidae. In prochilodontids the medial surface of the main body of the fourth epibranchial (E_4) in the region dorsal of the area where E_4 articulates with

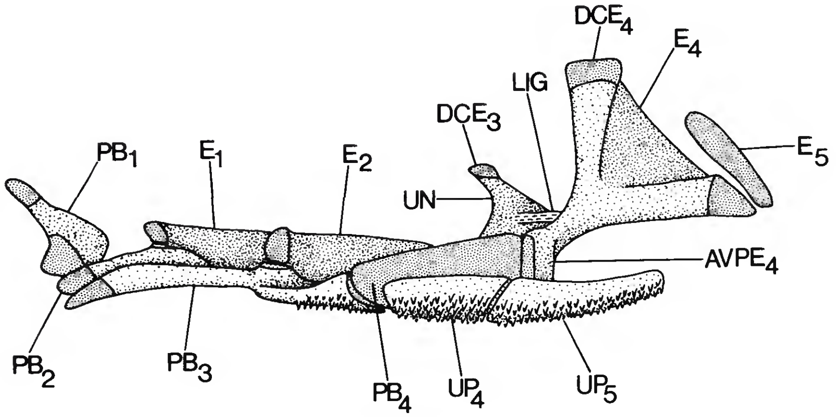

FIGURE 4.—*Xenocharax spilurus*, USNM 227693, dorsal portion of gill arches, right side, medial view, anterior to left (dense patterned stippling represents cartilage).

the fifth upper pharyngeal toothplate (UP_5) is flat and unelaborated (Figure 6). The primary axis of the dorsal process of the fourth epibranchial (the dorsal extension of Nelson, 1967, and the suprapharyngobranchial process of Bertmar et al., 1969) in prochilodontids has an anterodorsal orientation. The dorsal process of E_4 in that family terminates dorsally in a transversely flattened cartilage (DCE_4) that is relatively smaller than that in the Curimatidae and widely separated from the uncinate processes of the more anterior epibranchials (e.g., DCE_3, Figure 6). A cord-like ligament (LIG) extends between the posterior surface of the uncinate process of the third epibranchial (E_3) and the main body of the fourth epibranchial (E_4). That inter-epibranchial connective tissue band inserts in prochilodontids onto E_4 slightly posterolateral to the area of articulation of that element with the cartilaginous fourth infrapharyngobranchial (PB_4, Figure 6).

Analysis of the conditions of the fourth epibranchial in outgroups to the Curimatidae indicates that the form of the fourth epibranchial described in the preceeding paragraph represents the plesiomorphous state of the ossification. Those cited conditions are hypothesized to have been, in turn, the basis for a number of derived modifications of that ossification in a number of subunits of the Curimatidae.

The medial surfaces of the main body and dorsal process of the fourth epibranchial are unelaborated in all examined characiform outgroups. That simple condition, although also

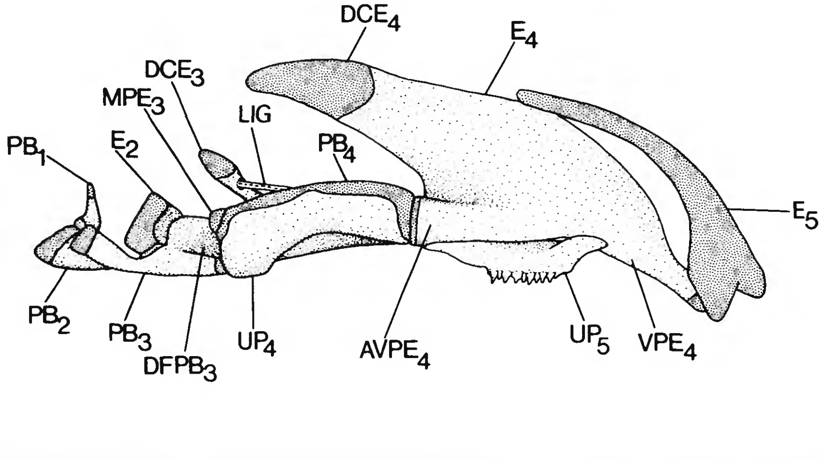

FIGURE 5.—*Curimatopsis microlepis*, MZUSP 21053, dorsal portion of gill arches, right side, medial view, anterior to left (dense patterned stippling represents cartilage).

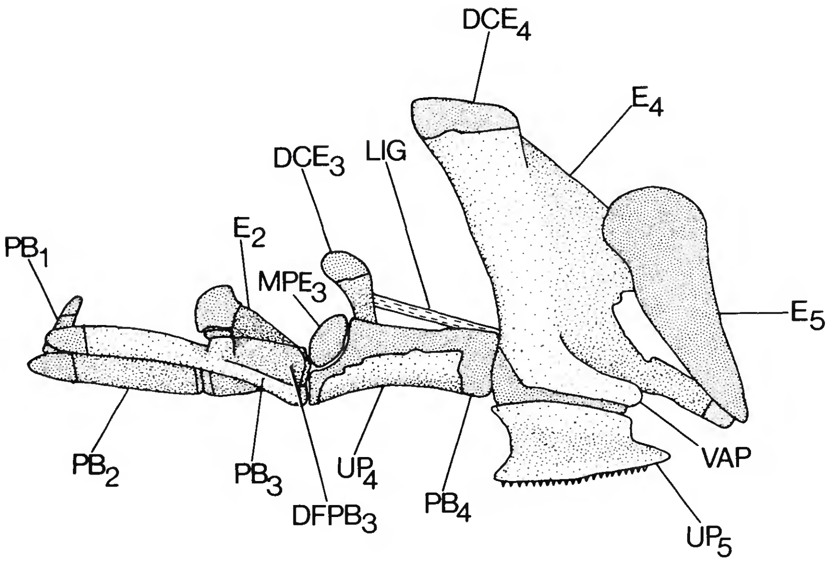

FIGURE 6.—*Prochilodus nigricans*, USNM 231438, dorsal portion of gill arches, right side, medial view, anterior to left (dense patterned stippling represents cartilage).

common to all members of the Prochilodontidae (Figure 6), is limited within the Curimatidae to the five species of the genus *Curimatopsis* (sensu Vari, 1982a,b) (Figure 5). In the genera *Potamorhina, Curimata, Psectrogaster, Steindachnerina, Pseudocurimata, Curimatella,* and *Cyphocharax* (Figures 7–11) a distinct posteroventrally sloping, often distally-tapering bony spur (MBS), or a further derived form of such a process, arises from the medial surface of the main body of the fourth epibranchial. The spur extends medially from the body of E_4 to varying degrees towards the midsagital plane, nearly contacting its counterpart of the other side in some subgroups of the family. The unique possession of this medial process of E_4 in *Potamorhina, Curimata, Psectrogaster, Steindachnerina, Pseudocurimata, Curimatella,* and *Cyphocharax* among the diverse characiform taxa examined is evidence of the derived nature of the possession of the spur. That process is consequently considered a synapomorphy for these seven genera (SYNAPOMORPHY 51). Although prochilodontids have an expansion of the ventral portion of the fourth epibranchial proximate to the cartilaginous articulation of E_4 and UP_5 (VAP, Figure 6), that elaboration differs both in position and form from the spur on the medial surface of the fourth epibranchial in *Potamorhina, Curimata, Psectrogaster, Steindachnerina, Pseudocurimata, Curimatella,* and *Cyphocharax*. The structure in the Prochilodontidae is consequently considered nonhomologous with the process in the cited curimatid genera.

The function of the medial spur arising from the body of the fourth epibranchial of most curimatids is uncertain. Although some connective tissue sheets attach to the spur, neither discrete well-developed ligaments nor muscles arise from that process. The dorsal surface of the spur does, however, contact and conform in shape to the proximate ventral region of the medial and posterior portions of the ventral surface of the muscular epibranchial organ common to all curimatids. Therefore the spur may serve, at least partially, as a support for the large epibranchial organ typical of the family. That functional hypothesis must be qualified by the observation that the Prochilodontidae, the sister group to the Curimatidae, along with the five species of the genus *Curimatopsis* have well developed epibranchial organs in the absence of a medial spur on the fourth epibranchial. Alternatively, the spur may function to some extent to stiffen a portion of the roof of the pharyngeal cavity. In the intact branchial basket of most curimatids the distal portion of the spur is an integral part of the roof of the pharyngeal cavity and stiffens that muscular tube directly (*Potamorhina, Psectrogaster, Steindachnerina, Pseudocurimata, Curimatella,* and *Cyphocharax*). In species of *Curimata* the spur is not directly integrated into the pharyngeal roof but rather supports the fifth upper pharyngeal tooth plate (see discussion below) which is, in turn, incorporated into the fleshy pharyngeal roof. Thus in both conditions the spur functions in reducing the flexibility of the fleshy upper portion of the pharyngeal cavity, a modification that presumably assists in maintaining contact between that region of the pharynx and the opposing dorsal surface of the fifth ceratobranchial during food item manipulation.

This medial bony process of the fourth epibranchial undergoes further apomorphous restructuring in some subgroups of non-*Curimatopsis* curimatids. These modifications serve to delimit several smaller assemblages within the family. The twelve nominal species assigned to *Psectrogaster* have the overall form of the medial spur of the fourth epibranchial significantly lengthened posteriorly (Figure 9) relative to the condition in the other members of the family with the structure. The unique nature of the elongation of the spur relative to the medially unelaborated E_4 typical of most characiforms, and with respect to the more moderately developed spur in other non-*Curimatopsis* curimatids is congruent with the hypothesis of the elongation being a synapomorphy for the species of *Psectrogaster* (SYNAPOMORPHY 86).

The spur on the fourth epibranchial in the species of *Curimata* differs from the form of the process in other curimatids in undergoing a progressive ontogenetic expansion ventrally. In the majority of curimatids with a medial spur on E_4 that process has a relatively small base where it arises from the medial surface of the fourth epibranchial. The ventral terminus of the base of the spur, in turn, is distinctly separated from the ventral articular surface of E_4. Similarly the ventral margin of the distal portions of the spur is distinctly separate to varying degrees from the medial margin of the fifth upper pharyngeal tooth plate.

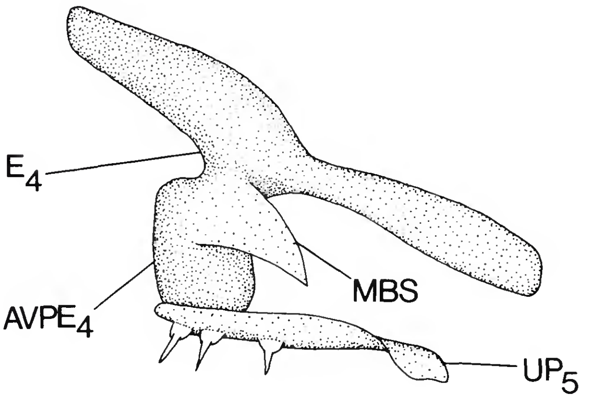

FIGURE 7.—*Curimata cyprinoides*, USNM 231433, juvenile, fourth epibranchial and fifth upper pharyngeal tooth plate, right side, medial view, anterior to left, both elements cartilaginous.

Juveniles of *Curimata cyprinoides* have a medial spur of the fourth epibranchial with an overall triangular form (Figure 7). At that stage in ontogeny the spur has a moderate area of attachment basally to the articular process of the bone ($AVPE_4$), a condition similar to that in adults of many non-*Curimatopsis* curimatids. During development the relatively narrow basal portion of the medial spur characteristic of juveniles of *Curimata* expands into a broad triangular sheet of bone extending ventrally to the margin of the articular surface between the fourth epibranchial and the fifth upper phargyneal tooth plate (Figure 8). As a consequence the basal portion of the spur in these taxa is continuous along an extensive vertical line with the medial surface of the ventralmost portion of the body of the fourth epibranchial. An additional consequence of that ontogenetic expansion is that specimens of species of *Curimata* of greater than approximately 40 mm SL have the ventral margin of the medial spur of the fourth epibranchial (MBS) in close proximity to the medial edge of the fifth upper pharyngeal tooth plate (UP_5). These two elements are furthermore relatively tightly attached by a connective tissue sheet. The dorsal margin of the E_4 spur in species of *Curimata* thickens progressively as the relative overall size of the spur increases; a process that ultimately forms a distinct undercut median shelf at the dorsal margin of the spur in the adults. The expanded median bony spur on E_4

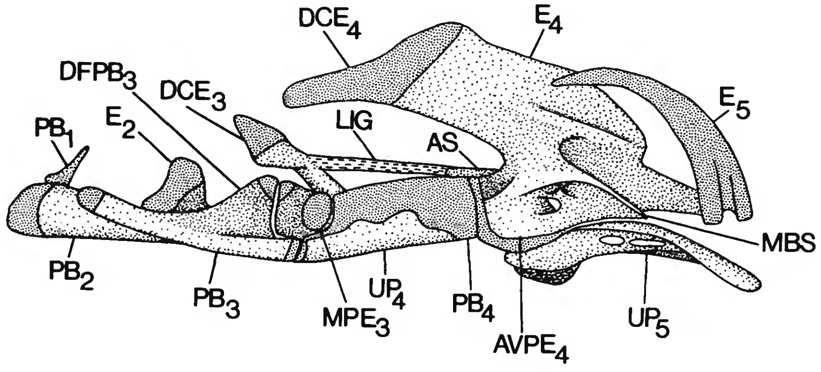

FIGURE 8.—*Curimata cyprinoides*, USNM 267964, dorsal portion of gill arches, right side, medial view, anterior to left (dense patterned stippling represents cartilage).

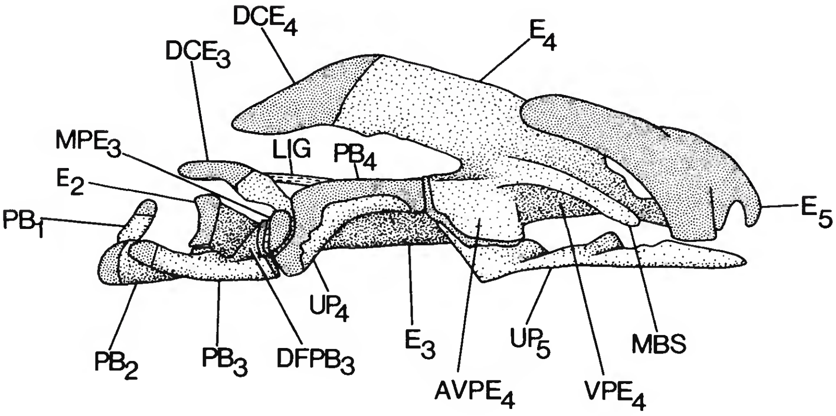

FIGURE 9.—*Psectrogaster curviventris*, USNM 243221, dorsal portion of gill arches, right side, medial view, anterior to left (dense patterned stippling represents cartilage).

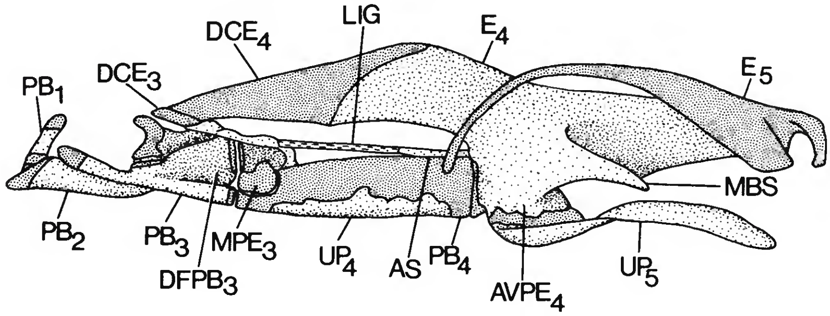

FIGURE 10.—*Potamorhina laticeps*, USNM 121325, dorsal portion of gill arches, right side, medial view, anterior to left (dense patterned stippling represents cartilage).

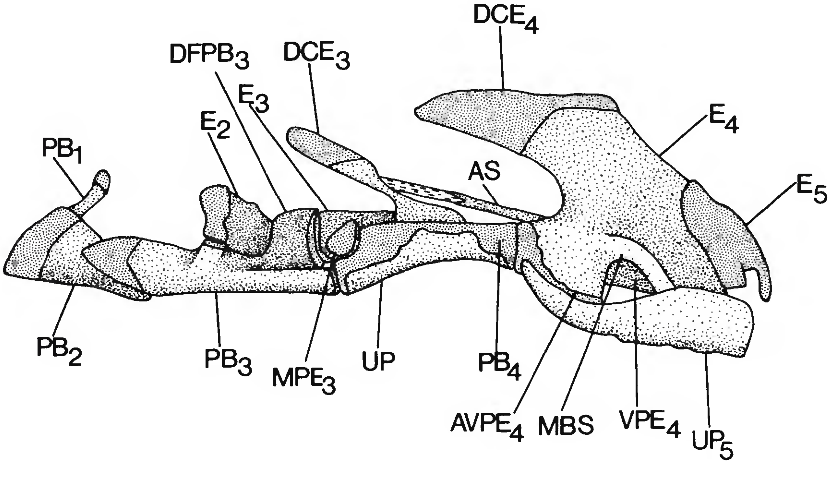

FIGURE 11.—*Steindachnerina hypostoma*, USNM 167802, dorsal portion of gill arches, right side, medial view, anterior to left (dense patterned stippling represents cartilage).

in adults of *Curimata* is also distinctive in its pronounced fenestration (Figure 8). Neither the dorsomedian shelf nor the fenestration of the fourth epibranchial spur are found in other curimatids.

The ontogenetic restructuring of the E_4 spur of *Curimata* from a condition comparable to that generalized for spur-bearing curimatids to the triangular plate characteristic of the genus is congruent with a hypothesis of the derived nature of that ossification (SYNAPOMORPHY 78). Similarly the development of a distinct dorsomedial shelf on the medial spur of the fourth epibranchial, and the fenestration of the spur are considered synapomorphous for the genus (SYNAPOMORPHY 79). Those ontogenetically derived polarity hypotheses are furthermore in agreement with data from outgroup analysis which also indicates that the possession of such elaborations of the fourth epibranchial spur are unique to, and represent synapomorphies for, the species of *Curimata*.

Apomorphous alterations of the dorsal portions of the fourth epibranchial, both ossified and cartilaginous, are notable within the Curimatidae. The form and orientation of the dorsal process of the fourth epibranchial generalized for, and hypothesized as primitive, within the Characiformes is a transversely flattened plate with a vertically or nearly vertically oriented central axis (Figure 4; Vari, 1983, fig. 15). Members of the Curimatidae (Figures 5, 7–11) and Prochilodontidae (Figure 6) are characterized by having that primary axis of the dorsal process of E_4 reoriented anterodorsally to some degree. That reorientation, apomorphous for the two-family clade (SYNAPOMORPHY 1), is least pronounced in the Prochilodontidae, but is more developed in some groups of curimatids as will be discussed below. The distal cartilaginous portion of the fourth epibranchial also varies in morphology within the Curimatidae. Outgroup studies indicate that the cartilage capping the dorsal process of E_4 is primitively a relatively small body as typified by the condition in *Xenocharax* Günther (Figure 4) and *Brycon* Müller and Troschel (Vari, 1983, fig. 15). That cartilage body on E_4 in the Prochilodontidae is somewhat, but not markedly, realigned anterodorsally relative to the condition in most characiforms. That shift and the comparable condition and more pronounced realignments within the Curimatidae together represent a synapomorphy for the Curimatidae and Prochilodontidae (SYNAPOMORPHY 2).

Within the Curimatidae further modifications are found both in the overall form of the dorsal process of E_4 and in the alignment and shape of its associated distal cartilage. The species of *Curimatopsis* are characterized by a distal cartilage of the fourth epibranchial that is similar in form to that in the Prochilodontidae; however, that genus has the primitively dorsal process of the fourth epibranchial more anterodorsally directed than in prochilodontids (Figure 5). That apomorphous anterodorsal reorientation of the dorsal process of E_4 is more pronounced in *Potamorhina, Curimata, Psectrogaster, Steindachnerina, Pseudocurimata, Curimatella,* and *Cyphocharax.* Those taxa have the primitively dorsal process of E_4 more anteriorly directed (Figures 8–11) than in either the Prochilodontidae (Figure 6) or *Curimatopsis* (Figure 5). As a consequence of this apomorphous reorientation, the transversely flattened cartilaginous terminal portion of the fourth epibranchial (DCE_4) constitutes the anterior limit of that element in non-*Curimatopsis* curimatids contrary to its dorsal location on the fourth epibranchial that is typical for characiforms. Congruent with the reorientation of the dorsal portion of E_4 is the anterior expansion of the distal cartilage on that element (DCE_4) into an elongate plate. In different phyletic lineages within the Curimatidae that plate extends anteriorly to varying degrees dorsal of the fourth infrapharyngobranchial and above the portions of the other gill arch elements located along the median margin of the dorsal half of the branchial complex (Figures 8, 9, 10, 12, 13).

The absence of comparable modifications of the primitively dorsal process of the fourth epibranchial and its associated terminal cartilage in characiform outgroups is congruent with the hypothesis that these alterations are shared derived characters for the Curimatidae and its subunits at two levels of generality. The moderate degree of anterodorsal alignment of the primary axis of the process in *Curimatopsis*, and the further derived more anterior alignment of the process in other curimatids together constitute a synapomorphy for the entire family (SYNAPOMORPHY 27). The pronounced anterior realignment, the more derived condition, in *Potamorhina, Curimata, Psectrogaster, Steindachnerina, Pseudocurimata, Curimatella,* and *Cyphocharax* is a derived synapomorphy of lesser generality within the family (SYNAPOMORPHY 52). The latter organization of the ossified and cartilaginous portions of E_4 is considered the condition from which further modifications of the fourth epibranchial in several less inclusive subunits of the Curimatidae are derived.

Among the species of *Potamorhina* the anteriorly reoriented dorsal process of the fourth epibranchial common to non-*Curimatopsis* curimatids is apomorphously further lengthened to a significant degree. This elaboration of the process results in a horizontally markedly elongate, vertical wall that extends medially along the anterolateral portion of the muscular epibranchial organ (Figure 10). The transversely-flattened cartilage (DCE_4) that caps the primitively dorsal, now anterior, portion of the bone is congruently significantly lengthened longitudinally in *Potamorhina*, and extends forward to contact the dorsal margin of the cartilage that caps the uncinate process of the third epibranchial (DCE_3). A distinct separation of these two cartilage bodies typifies other examined characiforms both outside of the Curimatidae (e.g., *Xenocharax spilurus* and *Prochilodus nigricans*, Figures 4, 6), and within the family (Figures 5, 8, 9, 11). The anterior lengthening of the dorsal process of the fourth epibranchial along with the close association of the cartilages of the third and fourth epibranchials in *Potamorhina* is consequently hypothesized to be synapomorphous for the members of the genus (SYNAPOMORPHIES 64 and 65).

The overall elongation of the fourth epibranchial in *Potamorhina* is paralleled by the anterior lengthening of the fifth epibranchial in the members of the genus. The fifth epibranchial (E_5) in most characiforms is typically a small cartilage at the posterior corner of the fourth epibranchial lying immediately posterodorsal of the junction of that element and the fourth ceratobranchial (e.g., *Xenocharax spilurus*, Figure 4). Both prochilodontids and curimatids have the cartilaginous E_5 expanded into a relatively large mass incorporated into the lateral wall of the large epibranchial organ. As noted by Vari (1983) the fifth epibranchial in those families is also noteworthy in its attachment to the posterodorsal margin of the fourth epibranchial, with a resultant encirclement by those elements of the fifth efferent branchial artery. Together this complex is considered a synapomorphy for the Curimatidae and Prochilodontidae (SYNAPOMORPHY 2). Within the Curimatidae the fifth epibranchial in *Potamorhina* (E_5, Figure 10) is further lengthened beyond the condition in prochilodontids and other curimatids into a long tapering body extending anteriorly to the level of the middle or posterior portion of the fourth infrapharyngobranchial, a synapomorphy unique to members of that genus (SYNAPOMORPHY 70).

All of the diverse groups of characiforms examined in the present study have a distinct cord-like ligament (LIG) that extends posteriorly from the rear margin of the uncinate process of the third epibranchial (E_3) to an attachment on the fourth epibranchial (E_4) (e.g., *Xenocharax spilurus* and *Prochilodus nigricans*, Figures 4, 6). This inter-epibranchial ligament attaches to E_4 at the anteriormost limit of the distinct ridge that extends along the lateral surface of the main body of the fourth epibranchial. In most characiforms that ridge on the fourth epibranchial terminates anteriorly just dorsal of the vertical plane through the area of contact of the fourth infrapharyngobranchial (PB_4) and the fourth epibranchial (Figure 12). The exact function of this inter-epibranchial ligament is uncertain, but it apparently limits the degree of flexure of the fourth epibranchial relative to the more anterior arches of the branchial apparatus, and is one of a series of comparable ligaments in the dorsal portion of the gill arches. Shorter, possibly serially homologous, ligaments also extend between the first epibranchial and the second infrapharyngobranchial, and between the second epibranchial and the third infrapharyngobranchial.

The five species of *Curimatopsis* have the ligament between the third and fourth epibanchials attached onto the relatively short ridge located on the anterolateral surface of the fourth epibranchial, an attachment comparable to the condition described above for characiform outgroups (Figure 12). The species of *Potamorhina, Curimata, Psectrogaster, Steindachnerina, Pseudocurimata, Curimatella,* and *Cyphocharax* rather than retaining a direct attachment of the ligament onto the main body of the fourth epibranchial have that band inserting onto a bony spur-like process (AS) that extends forward from the anterior margin of the main body of E_4 (Figures 8, 10, 11, 13, 14). The base of this bony spur corresponds in position to the region of E_4 where the E_3-E_4 ligament attaches in other characiforms. The spur, in turn, is longitudinally aligned along the axis of the ligament. Although the degree of development of the spur varies among those curimatids characterized by that process, the common possession of such an anterior extension of E_4 associated with the E_3-E_4 ligament is hypothesized to be a synapomorphy for the genera *Potamorhina, Curimata, Psectrogaster, Steindachnerina, Pseudocurimata, Curimatella,* and *Cyphocharax* given the absence of such an elaboration in examined outgroups (SYNAPOMORPHY 53).

Finally the overall form of the ventral portion of the fourth epibranchial is modified in all species of *Curimata*. In other curimatids, the portion of the fourth epibranchial that articulates with and supports UP_5 is situated directly ventral of the main body of E_4, and is in line with the vertical axis through the dorsal process of that element. In species of *Curimata*, alternatively, the ventral portion of E_4 is further shifted medially which results in an associated move towards

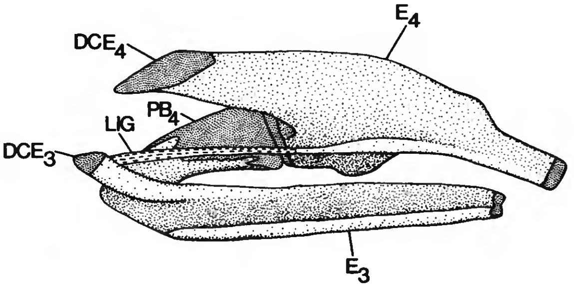

FIGURE 12.—*Curimatopsis microlepis*, USNM 268867, dorsal portion of third and fourth gill arches, left side, dorsolateral view, anterior to left (dense patterned stippling represents cartilage).

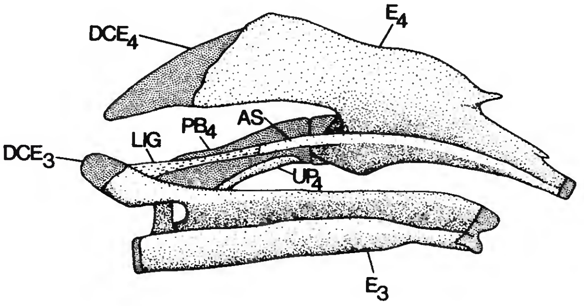

FIGURE 13.—*Curimatella alburna*, MZUSP 6309, dorsal portion of third and fourth gill arches, left side, dorsolateral view, anterior to left (dense patterned stippling represents cartilage).

the median plane of the attached fifth upper pharyngeal tooth plate (UP_5). As a consequence of this restructuring the complex consisting of the ventral portion of E_4 and the associated UP_5 in *Curimata* is located distinctly medial of the primary vertical plane through the dorsal section of the branchial apparatus (Figure 14) (SYNAPOMORPHY 80).

Fifth Upper Pharyngeal Tooth Plate (UP_5)

The ventral surface of the fifth upper pharyngeal tooth plate of most characiforms is typically relatively flat and dentigerous (e.g., *Brycon falcatus*, Figure 17, and *Xenocharax spilurus*, Figure 4). That tooth plate extends posteriorly a limited horizontal distance, from the posterior limit of the fourth upper pharyngeal tooth plate (UP_4) to the middle of the horizontal extent of the fourth epibranchial. The broad range in the form of the fifth upper pharyngeal tooth plate (UP_5) within the Curimatidae serves to define a number of subassemblages of the family. All members of the Curimatidae have the amount of dentition on the fifth upper pharyngeal tooth plate reduced, even in juveniles, relative to the condition in outgroups (Figures 5, 7–11), a derived feature (SYNAPOMORPHY 5). Both the fifth upper pharyngeal tooth plate and the associated dentition undergo further modifications within the family.

The shortest and least elaborate version of UP_5 occurs in the species of *Curimatopsis*. The tooth plate in that genus has a distinct patch of teeth on its ventral surface and a short dorsomedial shaft posteriorly (Figures 5, 15). The overall longitudinal dimension of UP_5 relative to E_4 is only somewhat longer than the state of that element typical of prochilodontids (e.g., *Prochilodus nigricans*, Figure 16) and examined characiform outgroups (e.g., *Brycon falcatus*, Figure 17). In the species of *Potamorhina, Curimata, Psectrogaster, Steindachnerina, Pseudocurimata, Curimatella* and *Cyphocharax* the fifth upper pharyngeal tooth plate is more elongate longitudinally (Figures 7–11) with the relatively short posterior shaft of the element characteristic of *Curimatopsis* lengthened to various degrees. The shape of the lengthened posterior portion of UP_5 mirrors the form of the region of the fifth ceratobranchial which it approximates when the dorsal and ventral portions of the gill arches are in contact. Although a number of genera of non-*Curimatopsis* curimatids have a variable number of teeth on the ventral surface of the fifth upper pharyngeal tooth plate as juveniles (Figure 7), the adults of those taxa are characterized by a pronounced reduction, or more typically an elimination of the dentition associated with UP_5. On the basis of outgroup comparisons both the increase in the relative length of UP_5, and the decrease in the amount of dentition on that tooth plate are hypothesized to be shared derived characters uniting *Potamorhina, Curimata, Psectrogaster, Steindachnerina, Pseudocurimata, Curimatella*, and *Cyphocharax* (SYNAPOMORPHY 54).

The apomorphous elongate form of UP_5 typical for non-*Curimatopsis* curimatids is further modified in various ways in some less inclusive subunits of the Curimatidae. Only one of these modifications is, however, derived for a group herein recognized at the generic level and thus appropriate for this discussion. Species of the genus *Psectrogaster* have an extremely elongate fifth upper pharyngeal tooth plate which extends caudally beyond the transverse plane through the posterior limit of the ossified portions of the gill arches (Figure 9). Such a posterior extension of the bone in *Psectrogaster* contrasts with the typical curimatid condition in which the fifth upper pharyngeal tooth plate barely reaches, or more usually falls distinctly short of, that transverse plane. The distal portion of UP_5 of species of *Psectrogaster* is also twisted along its

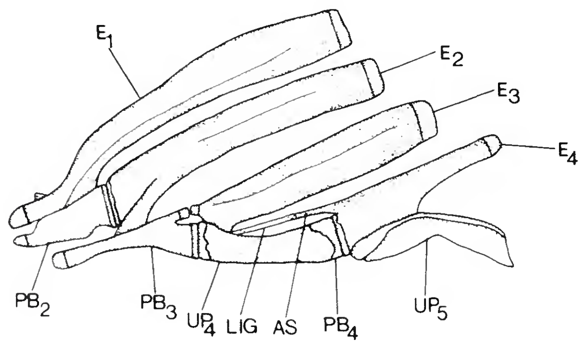

FIGURE 14.—*Curimata cyprinoides*, USNM 225619, dorsal portion of gill arches, left side, ventral view, anterior to left (dense patterned stippling represents cartilage).

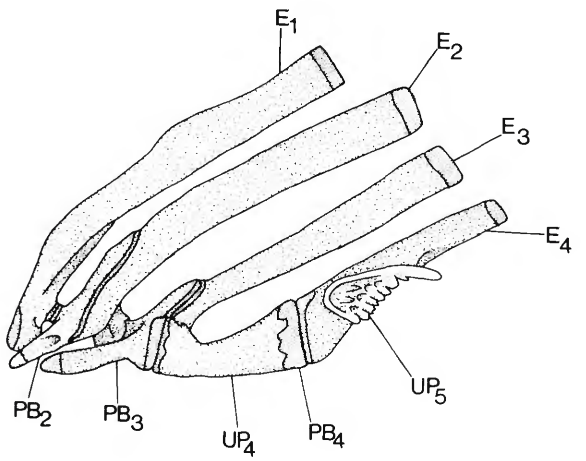

FIGURE 15.—*Curimatopsis microlepis*, MZUSP 21053, dorsal portion of gill arches, left side, ventral view, anterior to left (dense patterned stippling represents cartilage).

longitudinal axis, and is transversely expanded distally into an oar-shaped process; an apomorphous restructuring of the element again unknown elsewhere in the family. In light of the unique nature of the lengthening of UP_5 and its reconfiguration, the overall form of the bone is considered a derived character synapomorphous for the species of *Psectrogaster* (SYNAPOMORPHY 87).

Fourth Upper Pharyngeal Tooth Plate (UP_4) and Fourth Infrapharyngobranchial (PB_4)

In both the Curimatidae (Figure 15) and Prochilodontidae (Figure 16) an edentulous ossification envelopes most of the ventral surface and portions of the lateral margins of the cartilaginous fourth infrapharyngobranchial (PB_4). The homology of this ossification is somewhat problematical. It may represent a new perichondral element, with the fourth upper pharyngeal tooth plate (UP_4) usually attached to the ventral surface of the fourth infrapharyngobranchial being absent. Alternatively, the ossification along the ventral and lateral surfaces of PB_4 in the Curimatidae and Prochilodontidae may represent a restructured edentulous fourth upper pharyngeal tooth plate. The latter homology is tentatively proposed since it requires only one ad hoc hypothesis, the modification in the overall structure of UP_4. The alternative hypothesis, that the ossification represents a new perichondral element, necessitates two assumptions, the loss of UP_4 and the independent development of a new ossification on PB_4, a more complex scenario. A more definitive statement on the homology of the ossification on the ventral portion of PB_4 would necessitate presently unavailable ontogenetic information.

A definitive statement on the homology of the element is not crucial in terms of its phylogenetic significance. If the ossification is the fourth upper pharyngeal tooth plate it would, as was noted by Vari (1983:18), represent a pronounced restructuring of the plesiomorphous plate-like UP_4 (Figure 17) that typically contacts only the ventral surface of PB_4 in most characiforms. Similarly a new perichondral ossification on the ventral surface of PB_4 and the loss of UP_4 would also be derived. The expanded curved ossification on PB_4 was consequently considered derived by Vari (1983) and a synapomorphy for the Curimatidae and Prochilodontidae (SYNAPOMORPHY 4). Subsequent outgroup analysis has shown that the overall profile of the resultant UP_4-PB_4 bone-cartilage complex in those families is also phylogenetically informative. The typical, and hypothesized plesiomorphous, form of the fourth infrapharyngobranchial in characiforms has a relatively straight or moderately convex lateral margin when viewed from a ventral view. That form of PB_4 is common to the majority of characiforms including several diverse families: Citharinidae (*Citharinus* Cuvier); Distichodontidae (*Neolebias* Steindachner (Vari, 1979:305), *Mesoborus* Pellegrin, and *Xenocharax*); Characidae, including genera from the Neotropics (*Agoniates* Müller and Troschel, *Brycon* (Figure 17), *Clupeacharax*, *Exodon* Müller and Troschel, *Hollandichthys* Eigenmann) and the Old World (*Alestes* Müller and Troschel, *Hydrocynus* Cuvier (Brewster, 1986, fig. 14), *Phenacogrammus*); Chilodontidae (*Caenotropus* Günther (see Vari, 1983, figs. 18, 19)); Hemiodontidae (*Hemiodopsis* Fowler); and Parodontidae (*Parodon* Valenciennes). In all examined members of the Curimatidae and Prochilodontidae the anterior portion of PB_4 and the associated anterior section of UP_4 are transversely expanded laterally which results in the overlap of the anteromedial surface of the third epibranchial (E_3) by the

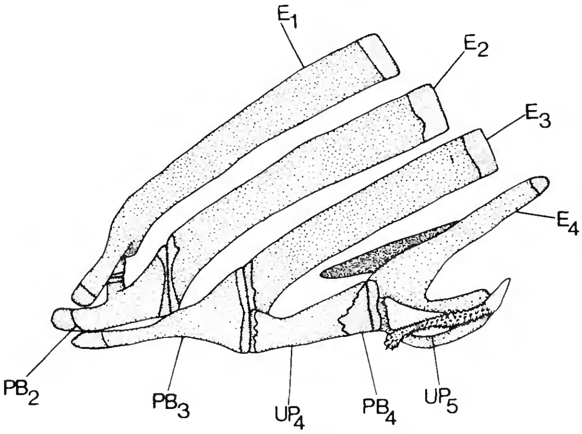

FIGURE 16.—*Prochilodus nigricans*, USNM 231438, dorsal portion of gill arches, left side, ventral view, anterior to left (dense patterned stippling represents cartilage).

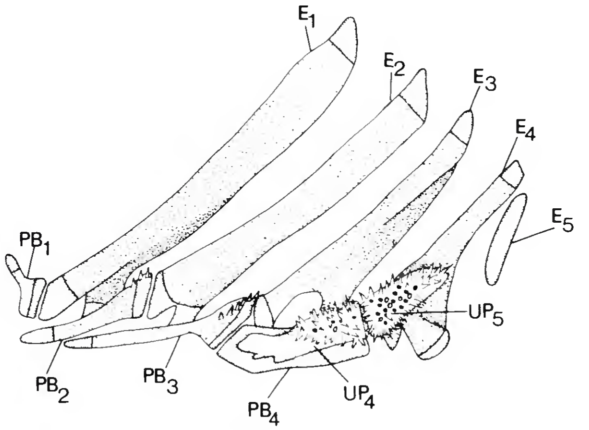

FIGURE 17.—*Brycon falcatus*, USNM 226161, dorsal portion of gill arches, left side, ventral view, anterior to left (dense patterned stippling represents cartilage).

conjoined PB_4 and UP_4. As a consequence of this anterior expansion, the PB_4-UP_4 complex appears transversely constricted midway along its longitudinal length (Figures 15, 16) contrary to the relatively parallel, or outwardly bowed lateral margin of that complex in other examined characiforms (e.g., *Brycon falcatus*, Figure 17). Outgroup comparisons have failed to reveal comparable modifications in other examined characiforms, and the form of the PB_4-UP_4 bone-cartilage complex is thus considered synapomorphous for the members of the Curimatidae and Prochilodontidae (SYNAPOMORPHY 12).

The form of the conjoined UP_4-PB_4 common to curimatids and prochilodontids is further modified in one generic level subunit of the Curimatidae. *Potamorhina* species have both the fourth infrapharyngobranchial and the associated fourth upper pharygneal tooth plate significantly lengthened longitudinally (Figure 10). That adaptation is considered derived (SYNAPOMORPHY 66) with respect to the relatively shorter form of these elements in other curimatids and the families that constitute the nested sister groups to the Curimatidae .

Third Epibranchial (E_3)

The dorsal portion of the third branchial arch consists of two bones, the third epibranchial (E_3) and third infrapharyngobranchial (PB_3) along with their associated cartilages. Derived modifications of those elements unite the Prochilodontidae and Curimatidae, and define lineages within the latter family. The apomorphous modifications of the third epibranchial will be discussed first.

The generalized form of the third epibranchial among characiforms has a cartilage capped uncinate process (UN) whose distal portion (DCE_3) terminates both distinctly lateral of the median plane of the gill arches, and posterior of the junction of the third infrapharyngobranchial with the third epibranchial and fourth infrapharyngobranchial (Figures 4, 18). All members of the Curimatidae and Prochilodontidae have the uncinate process of the third epibranchial markedly modified. In those two families the uncinate process is oriented anteriorly (Figure 19) rather than retaining the lateral or slightly anterolateral alignment found in other characiforms (Figure 18). As a consequence of this realignment the uncinate process with its associated distal cartilage overlays the vertical plane through the articulation between PB_3 and E_3 rather than terminating distinctly posterior of that articulation. The uncinate process additionally more closely approaches the median plane of the arches than is typical in characiform outgroups. Correlated with these changes is the approximation with the uncinate process to the midventral basal portion of the neurocranium to which it is attached by a ligamentous band. Together these hypothesized derived modifications are considered a synapomorphy for the Curimatidae and Prochilodontidae (SYNAPOMORPHY 13).

The anterior portion of the main shaft of E_3 in characiform outgroups is capped anteriorly by a relatively large articular cartilage that contacts the lateral half of the posterior margin of the cartilaginous third infrapharyngobranchial (PB_3). Medially that cartilage cap of the third epibranchial (ASE_3, Figure 18) slightly overlies and abuts the dorsolateral surface of the fourth infrapharyngobranchial (PB_4), but is distinctly separated from the midsagittal plane. The anterior portion of the main shaft of E_3 in the Curimatidae and Prochilodontidae is significantly modified relative to that generalized bauplan.

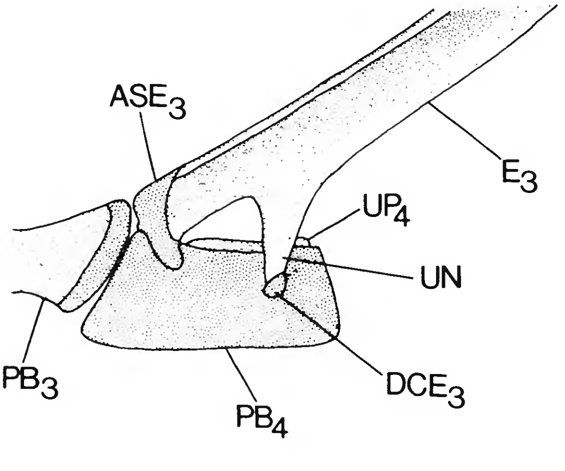

FIGURE 18.—*Brycon falcatus*, USNM 226161, fourth infrapharyngobranchial, posterior portion of third infrapharyngobranchial, and anterior portion of third epibranchial, right side, dorsal view, anterior to left (dense patterned stippling represents cartilage).

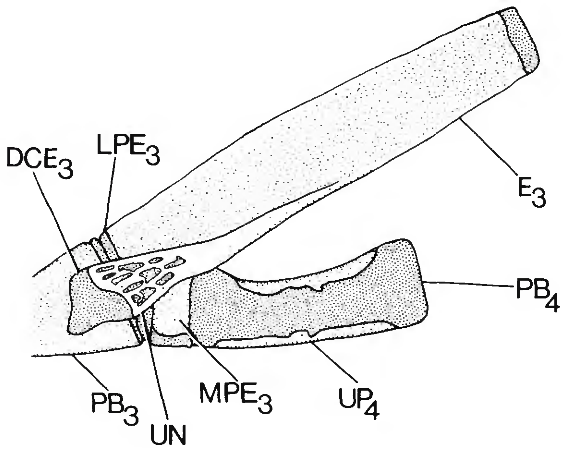

FIGURE 19.—*Curimata cisandina*, USNM 229171, fourth infrapharyngobranchial, fourth upper pharyngeal tooth plate, posterior portion of third infrapharyngobranchial, and third epibranchial, right side, dorsal view, anterior to left (dense patterned stippling represents cartilage).

Rather than terminating as a single articular surface along the posterolateral margin of the third infrapharyngobranchial, the articular surface of the third epibranchial in the Curimatidae and Prochilodontidae is divided into two subsections. The anterolateral margin of E_3 retains contact with the cartilage along the posterolateral portion of PB_3 (LPE_3, Figure 19). In contrast, the relatively small medial extension of the anterolateral portion of the third epibrancial that characteristically extends over the dorsolateral surface of the fourth infrapharyngobranchial of most characiforms is totally altered in these two families. Curimatids and prochilodontids have the medial extension expanded into a relatively thick ossified process (MPE_3, Figure 19) which extends over the anterodorsal portion of the fourth infrapharyngobranchial and terminates medially in a relatively large cartilage cap. This medially expanded process extends along and is surrounded posteroventrally by a matching groove in the anterodorsal surface of the cartilaginous fourth infrapharyngobranchial (PB_4). As a consequence the medial process of the third epibranchial in both families is visible in a medial view of the dorsal portions of the gill arches (Figures 5, 6, 8–11). The lateral expansion and ossification of the medial process of the third epibranchial, and associated reconfiguration of the proximate portion of PB_4 in the Curimatidae and Prochilodontidae are considered derived relative to the condition of these elements in other characiforms, and together represent a synapomorphy for those families (SYNAPOMORPHY 14).

A medial elongation of the anterior portion of PB_3 also occurs among characiforms in the Anostomidae (Vari, 1983, fig. 20), Chilodontidae (Vari, 1983, fig. 19), Hemiodontidae, and Parodontidae. None of the cited families has the third epibranchial terminating anteriorly in a large medial process comparable to that of the Curimatidae and Prochilodontidae. With the exception of the Chilodontidae (*Chilodus* Müller and Troschel, *Caenotropus*) and a single genus in the Hemiodontidae (*Bivibranchia* Eigenmann, sensu Vari, 1985), the cartilage along the anteromedial portions of the articular surface on the third epibranchial in these families is continuous with the lateral portion of that cartilage contacting the fourth infrapharyngobranchial. Such continuity contrasts with the subdivision of that cartilage cap into two independent masses in the Curimatidae and Prochilodontidae. As noted, the Chilodontidae has two distinct distal cartilages on the anterior portion of E_3 (e.g., *Caenotropus*, Vari, 1983, fig. 19). The medial section of that portion of the bone, however, consists of a slender shaft approximating but not reaching the medial plane, a significantly different condition than that found in the Curimatidae and Prochilodontidae.

Furthermore the Chilodontidae shares numerous synapomorphies with, and is evidently most closely related to the Anostomidae (Vari, 1983:50) which lacks comparable derived restructurings of the anterior portion of the third epibranchial. The medial process of the third epibranchial in *Bivibranchia* more closely approximates the form of the structure in the Curimatidae and Prochilodontidae, but differs from the condition in those families in details of its site of origin and overall morphology. Moreover, *Argonectes* Böhlke and Myers, which is evidently the closest relative of *Bivibranchia* (Roberts, 1974), together with all the other members of the Hemiodontidae lack such a distinct medial process on E_3. The noted differences in the structure of the third epibranchial in the Curimatidae and Prochilodontidae versus those in the Chilodontidae and *Bivibranchia*, in conjunction with the data on phylogenetic relationships of those taxa (Vari, 1983; Roberts, 1974) make it simplest to assume that the modifications in the Chilodontidae and *Bivibranchia* are non-homologous with the described alterations of the third epibranchial hypothesized synapomorphous for the Curimatidae and Prochilodontidae.

All members of the Curimatidae have at least a slight ridge along the ventral surface of E_3 extending in line with the longitudinal axis of the element. This ridge is further elaborated in two subunits of the family. A well developed ridge is characteristic of all members of *Psectrogaster* (SYNAPOMORPHY 88). Similarly a very strong ventral ridge on E_3 is shared by a clade consisting of three nominal species within *Curimata* (*aspera*, *simulata*, and *cerasina*); an elaboration which in those species parallels the ridge on the opposing dorsal surface of the third ceratobranchial of the ventral portion of the branchial basket. The common possession of the ventral ridge in *Psectrogaster* and a subunit of *Curimata* is considered homoplasious in the overall most parsimonious scheme of relationships within the family, although synapomorphous for each of those clades (see “Synapomorphy List and Phylogenetic Reconstruction” and “Convergent Characters”).

Third Infrapharyngobranchial (PB_3)

The third infrapharyngobranchial (PB_3) is typically a flattened or slightly dorsally concave, longitudinally elongate triangular bone in characiforms. As a consequence of its flattened form the ossification lies entirely or nearly entirely in the horizontal plane through the ventral surface of the upper portions of the gill arches. The lateral portion of PB_3 is consequently not visible or only slightly visible in a medial view of that complex (e.g., *Xenocharax spilurus*, Figure 4). Such a flattened PB_3 characterizes the Anostomidae and Chilodontidae which together constitute the sister clade to the lineage formed by the Prochilodontidae and Curimatidae. The Prochilodontidae and Curimatidae rather than retaining the flattened PB_3 of other characiforms have the posterolateral portion of the ossification restructured into a vertically or near vertically aligned flange that extends distinctly dorsal of the horizontal plane through the ventral main portion of the ossification. This restructuring results in the lateral portion of the bone being readily visible in a median view of the gill arches in both curimatids and prochilodontids ($DFPB_3$, Figures 5, 6, 8–11). The unique nature of this modification of the third pharyngobranchial in those two families is indicative of the derived nature of the character and is another derived attribute supporting the hypothesis of the monophyly of the clade formed by the Curimatidae and Prochilodontidae (SYNAPOMORPHY 15).

The association of the third infrapharyngobrancial (PB_3) with its respective epibranchial (E_3) and of PB_3 with the fourth infrapharyngobranchial (PB_4) varies within the family Curimatidae. The form of PB_3 typical for characiforms has a continuous articular cartilage along its posterior margin. The medial portion of the posterior PB_3 cartilage contacts the anterior margin of the cartilaginous PB_4, and the lateral portion of that cartilage of PB_3 abuts the articular cartilage that caps the anterior section of E_3 (Figure 16, 17). In most characiforms the joint of PB_3 with PB_4 and E_3 is either transversely straight (Figure 16) or at a slight angle (Figure 17), but there is no pronounced overlap of PB_3 lateral to the ossified portion of E_3. All *Curimatopsis* species (Figure 15), in contrast, have the joint between the third infrapharyngobranchial and third epibranchial distinctly oblique relative to a transverse plane through the branchial basket. As a consequence of the restructuring the posterolateral portion of the third infrapharyngobranchial apomorphously extends posteriorly into the region primitively occupied by the anterolateral portion of the third epibranchial (compare Figures 15–17), a derived condition (SYNAPOMORPHY 43). The overlap between these elements found in some members of the Old World characiform family Distichodontidae (e.g., *Mesoborus*) is a function of the posterolateral development of a process of PB_3 that extends lateral of the anterolateral edge of the ossified portion of E_3 rather than a consequence of the realignment of the PB_3-E_3 joint, and thus is non-homologous with the condition in *Curimatopsis*.

As noted, it appears that a continuous cartilage cap along the posterior margin of the third infrapharygobranchial is the primitive condition of that element in characiforms. Such an articular surface is common to the Prochilodontidae (Figure 16), New and Old World members of the Characidae (e.g., *Brycon*, Figure 17), the Hemiodontidae, Hepsetidae, Citharinidae, Distichodontidae, and other characiform outgroups examined. Such a continuous cartilage cap on PB_3 is also characteristic of all members of *Curimatopsis* (Figure 15) in the Curimatidae. In the species of *Potamorhina, Curimata, Psectrogaster, Steindachnerina, Pseudocurimata, Curimatella,* and *Cyphocharax* this hypothesized plesiomorphic single cartilage mass on PB_3 is subdivided sagitally (SYNAPOMORPHY 55). The medial portion of the cartilage mass of the third infrapharyngobranchial articulates with the anterior surface of the fourth infrapharygobranchial. The lateral section of the cartilage, located along the dorsal flange of the third infrapharyngobranchial ($DFPB_3$), contacts the anterior articular cartilage of E_3 (Figures 8, 10, 11). A distinct ossified region along the posterior border of the third infrapharyngobranchial separates these two cartilage masses.

Although hypothesized to be a derived character common to all genera other than *Curimatopsis* within the Curimatidae, a subdivision of the posterior articular cartilage on the third infrapharyngobranchial is not unique to that assemblage among characiforms. The transversely widened PB_3 of the Chilodontidae and Anostomidae demonstrates a similar fission of the posterior cartilage mass (see Vari, 1983, figs. 18, 19). Within the Hemiodontidae, a comparable transversely divided articular surface is limited to *Bivibranchia* (sensu Vari, 1985). The overall hypothesis of relationships for the Curimatidae, Prochilodontidae, Anostomidae, and Chilodontidae (Vari, 1983) indicates that the common presence of a subdivided PB_3 cartilage in the majority of the genera in the Curimatidae, and in the clade consisting of the Anostomidae and Chilodontidae may represent a homoplasious independent acquisition of that derived feature in those two lineages. An alternative hypothesis is its loss in the ancestors of the Prochilodontidae and in the lineage consisting of *Curimatopsis*; or by the fusion of those cartilage bodies in the common ancestor of Curimatidae and Prochilodontidae and the subsequent fission of the cartilage in non-*Curimatopsis* curimatids. The hypothesis of the independent acquisition of a subdivided cartilage in the clade formedby the Anostomidae and Chilodontidae, and in non-*Curimatopsis* curimatids proposed in this study is more parsimonious by one step than the cited possible alternative ad hoc hypotheses. Thus, the possession of two discrete articular cartilages on the posterior of PB_3 is considered a synapomorphy for *Potamorhina, Curimata, Psectrogaster, Steindachnerina, Pseudocurimata, Curimatella,* and *Cyphocharax.*

The hypothesis of the independent acquisition of a subdivided PB_3 articular cartilage within and outside of the Curimatidae can also be applied from a functional basis. In the Chilodontidae and Anostomidae the subdivision of the articular cartilage is apparently correlated with the pronounced transverse widening of the third infrapharyngobranchial. Such a transverse expansion of the third infrapharyngobranchial is not found in *Potamorhina, Curimata, Psectrogaster, Steindachnerina, Pseudocurimata, Curimatella,* and *Cyphocharax* that rather demonstrate a dorsal expansion of the lateral region of the bone. The common possession of a subdivided posterior articular cartilage in non-*Curimatopsis* curimatids and *Bivibranchia* is similarly considered homoplasious. Available data indicates that *Bivibranchia* is a highly modified member of the *Hemiodontidae* that is evidently most closely related to *Argonectes* (Roberts, 1974:432). Neither *Argonectes,* the presumed sister group to *Bivibranchia,* nor any other of the examined hemiodontid genera (*Anodus, Hemiodopsis, Hemiodus* Müller and Troschel, *Micromischodus* Roberts) have the transverse development of the medial portion of PB_3 typical of *Bivibranchia,* nor do they have the transverse subdivision of the posterior articular cartilage on that element that characterizes that genus. It is thus simplest to consider the presence of a subdivided PB_3 articular surface in *Bivibranchia* as being independently acquired and thus not homologous to the similar modifications in non-*Curimatopsis* curimatids.

Second Branchial Arch

The second epibranchial (E_2) and second infrapharyngobranchial (PB_2) of characiforms typically articulate along a plane nearly transverse to the main longitudinal axis of the branchial complex. The second epibranchial ranges from rounded to somewhat V-shaped in cross section, but with its ventral margin rounded in either case. The second infrapharyngobranchial is flanked anterolaterally by the anteromedial portion of the first epibranchial, and along its medial surface contacts the lateral surface of the anterior half of the third infrapharyngobranchial. The contact between these elements is strengthened by ligamentous connections, but not via elaborations of the ossified portion of PB_2.

The complex consisting of the second epibranchial and the second infrapharyngobranchial exhibits within the Curimatidae some modifications similar to those that occur on the third branchial arch in that family. The angled area of contact noted above for the third epibranchial and third infrapharyngobranchial in *Curimatopsis* is paralleled and indeed carried even further on the second gill arch (Figure 15). All *Curimatopsis* species have a significant reduction of the anterolateral margin of the second epibranchial. The lateral margin of PB_2 in the species of that genus is, in turn, expanded laterally into the region occupied in other characiforms and curimatids by the anterolateral portion of E_2. This significantly increases the size of PB_2 and results in a unique transversely angled articulation between the second epibranchial and second infrapharyngobranchial. These conditions are together considered a snyapomorphy for the genus (SYNAPOMORPHY 44).

All species of *Psectrogaster* have longitudinally aligned ridges along the ventral surface of the second epibranchial comparable to those of the third epibranchial. These ridges, which contrast with the ventrally unelaborated second epibranchial generalized for characiforms, are another derived character hypothesized synapomorphous for the members of the genus (SYNAPOMORPHY 89). Similar ridges are found in a subunit of *Curimata* (*mivartii, cerasina, aspera, simulata, alleni, cisandina,* and two undescribed species). As in the case of the ridge on the third epibranchial, the most parsimonious hypothesis of relationships within the Curimatidae (see "Synapomorphy List and Phylogenetic Reconstruction" and "Convergent Characters") indicates that the ridges in *Psectrogaster* and the cited subunit of *Curimata* represent independent acquisitions of those elaborations.

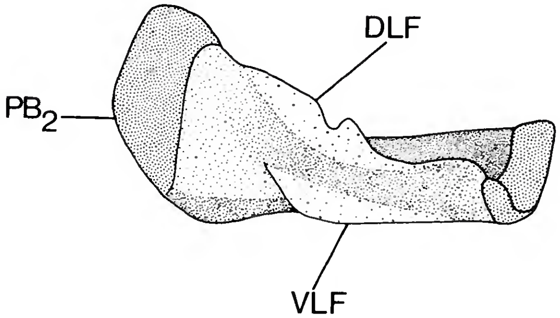

FIGURE 20.—*Steindachnerina hypostoma*, USNM 167802, second infrapharyngobranchial, right side, posterior view, medial to left (dense patterned stippling represents cartilage).

The medialmost element of the dorsal portion of the second branchial arch, the second infrapharyngobranchial (PB_2) also demonstrates various derived modifications. The posterolateral elaboration of the element associated with the expansion of the articular surface between the second infrapharyngobranchial and second epibranchial in *Curimatopsis* was noted above. In the species of *Steindachnerina* the anteromedial surface of the third infrapharyngobranchial fits into a depression on the lateral surface of the second infrapharyngobranchial (PB_2) (Figure 20). Ventrally PB_2 has an ossified shelf (VLF) extending along the ventral margin of PB_3 and dorsally there is a vertical plate (DLF) extending along the medial surface of that element. These processes are moderately developed in the nominal species and subspecies *S. argentea, S. conspersa, S. bimaculata, S. trachysteta, S. bimaculata sialis, S. pterostigma, S. semiornata, S. melanira, S. leucisca leucisca, S. leucisca bolivae,* and *S. binotata,* and more elaborately developed in the remaining members of the genus. The possession of such processes whether moderately or well developed is considered a synapomorphy for the genus (SYNAPOMORPHY 97).

Psectrogaster species also have a distinct flange on the dorsal surface of PB_2 (SYNAPOMORPHY 90) comparable to that in *Steindachnerina,* particularly those species of *Steindachnerina* with the more elaborate vertical development of the flange. However *Psectrogaster* lacks the ventral shelf overlapping the ventral surface of PB_3. Although comparable in overall form, I consider the similarly placed dorsal processes on the lateral surface of the second infraphyarngobranchial in *Steindachnerina* and *Psectrogaster* to be homoplasious within the context of the overall most parsimonious hypothesis of relationships (see "Convergent Characters").

First Branchial Arch

The typical characiform first branchial arch has a ventrally unelaborated first epibranchial (E_1) and a moderate sized first infrapharyngobranchial (PB_1) whose cartilaginous basal section is smaller than the ossified portion which typically forms the dorsal section of that element. The dorsally located uncinate process of the first epibranchial extends from the anteromedial surface of E_1, having the form of a discrete process terminating anteriorly in a cartilaginous body that contacts a corresponding cartilage on the dorsal surface of the uncinate process of the second infrapharyngobranchial (PB_2).

Both of the elements of the first branchial arch, the first infrapharyngobranchial and first epibranchial, demonstrate apomorphous modifications within the Curimatidae. In all members of *Curimata*, PB_1 is either proportionally reduced in size compared to the moderate sized PB_1 typical of most characiforms, or is completely lacking. This progressive reduction and loss of the first infrapharyngobranchial is hypothesized as derived given the condition in the outgroups, and is thus a synapomorphy for the species of *Curimata* (SYNAPOMORPHY 81). *Steindachnerina* species do not demonstrate any marked changes in the ossified portion of the first infrapharyngobranchial, but the medial cartilaginous section of the element is greatly enlarged, being more extensive than the ossified portion of the first infrapharyngobranchial and contacting the anterior portions of both the first epibranchial and second infrapharyngobranchial. This condition represents an evidently derived state relative to the morphology of those components common to other curimatids in which the ossified portion of the first infrapharyngobranchial is the larger, and wherein the first and second infrapharyngobranchials are typically not in contact (SYNAPOMORPHY 98).

The typical first epibranchial in characiforms is V-shaped in cross section and most commonly unelaborated on its ventral surface. A well-developed ridge on the ventral surface of E_1 is typical for the species of *Psectrogaster*, a hypothesized derived condition given the absence of such an elaboration in characiform outgroups (SYNAPOMORPHY 91). A longitudinal ridge is also present ventrally on the E_1 of *Curimata* species, but ranges within that genus in its degree of development. The well-developed ridge comparable to that of *Psectrogaster* occurs only in two species of *Curimata* and the overall most parsimonious hypothesis of relationships within the Curimatidae indicates that the presence of such a ridge in *Curimata* is non-homologous with the ridge characteristic of *Psectrogaster* species (see "Synapomorphy List and Phylogenetic Reconstruction" and "Convergent Characters").

Outgroup studies indicate that the first epibranchial in characiforms has a small to moderate sized, dorsally located uncinate process that terminates in a single cartilaginous cap which contacts a corresponding articular cartilage on the dorsal surface of the second infrapharyngobranchial. *Potamorhina* species, in contrast, have a well developed E_1 uncinate process which has two distinct subsections distally, each terminating in a distal cartilage cap (UN, Figure 21) (SYNAPOMORPHY 71). The anterior of the two articular surface contacts the matching cartilage body on the uncinate process that arises from the anteroventral portion of PB_2. The posterior cartilage-capped articular surface of the uncinate process of E_1 extends dorsally from the main body of the process at an angle of approximately 45° relative to its partner and approximates the neurocranium dorsally. Two separate articular surfaces on the uncinate process of E_1 also occur in all nominal species of *Curimata* other than *C. ocellata*, *C. semitaeniata*, *C. vittata*, *C. murieli*, and *C. macrops*. The subdivided cartilage cap on the E_1 uncinate process of most *Curimata* species differs, however, from the state in *Potamorhina* in its overall morphology and details of its spatial relationships with the second infrapharyngobranchial. Within *Curimata* it is also possible to follow the ontogenetic and phylogenetic expansion of the distal portion of the uncinate process of E_1, and the fission of its articular surface into two subunits. No internal evidence of such a subdivision exists for the species for *Potamorhina*, and it is possible that the situation in that genus does not represent a subdivision of the original cartilaginous articular surface, but rather the de novo development of a second cartilage body on the uncinate process. Furthermore, the overall hypothesis of relationships within the Curimatidae indicates that these two cartilage-capped surfaces on the E_1 uncinate process in *Potamorhina* and a subunit of *Curimata* are independently achieved (see "Synapomorphy List and Phylogenetic Reconstruction").

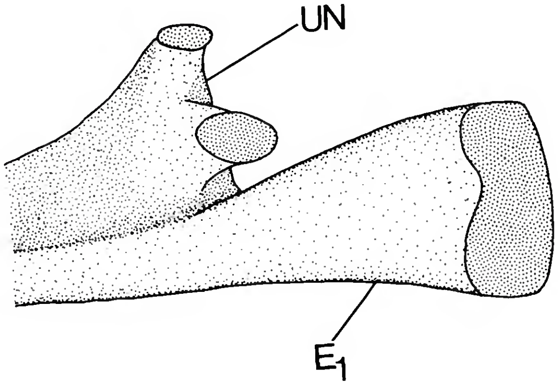

FIGURE 21.—*Potamorhina squamoralevis*, USNM 243228, first epibranchial, right side, anterior portion, posterior view, median plane to right (dense patterned stippling represents cartilage).

Ventral Portion of Branchial Arches

Although not demonstrating such dramatic derived restructurings as are found in the dorsal portions of the gill arches, the ventral elements of the branchial basket have a number of modifications pertinent to the question of the monophyly of the Curimatidae and relative to the relationships of its constituent genera. In the following discussion, the analysis is arranged around subunits of the arches that typically consist of individual elements.

First Basibranchial (BB_1)

The generalized condition for characiforms is the possession of a distinct, typically rod-shaped, medial first basibranchial situated posterior of the basihyal and anterior of the second basibranchial. As noted by Vari (1983:14) prochilodontids have a small triangular first basibranchial that abuts the anterior margin of the second basibranchial and which barely extends to the level of the first hypobranchial (see Vari, 1983, fig. 9). A recognizable first basibranchial is, in turn, lacking in all curimatids (Figure 25). This reductive trend is hypothesized to be apomorphous at two levels of universality. The reduction of the first basibranchial or the absence of that element as a discrete ossification are together considered a synapomorphy for the Prochilodontidae and Curimatidae (SYNAPOMORPHY 6). The absence of an ossified first basibranchial is, in turn, considered a synapomorphy for the members of the family (SYNAPOMORPHY 19) (see Vari, 1983:14 for a further discussion of this complex).

Second Hypobranchial (H_2)

The articular cartilaginous surface of the second hypobranchial of most characiforms consists of two subunits, a smaller cartilage body at the anterolateral corner of the ossification and an extensive cartilage along the medial and posterior portions of the bone (Figure 22A). This morphology is found in the Anostomidae, Chilodontidae, and Prochilodontidae, and among curimatids also occurs in the genus *Curimatopsis*. *Potamorhina* species retain two separate cartilages anteriorly, but the separation between them is considerably reduced (Figure 22B). The genera *Curimata, Psectrogaster, Steindachnerina, Pseudocurimata, Curimatella,* and *Cyphocharax* have a continuous cartilage body extending along the anterior and at least part of the medial surface of the element (Figure 22C) rather than two separate cartilages. In light of the broad separation anteriorly of the cartilages on the second hypobranchial in characiform outgroups, the reduction or elimination of the gap between the two anterior cartilages is considered a synapomorphy for the members of *Potamorhina, Curimata, Psectrogaster, Steindachnerina, Curimatella,* and *Cyphocharax* (SYNAPOMORPHY 56). The fusion of the two anterior cartilages into a continuous body in *Curimata, Psectrogaster, Steindachnerina, Pseudocurimata, Curimatella,* and *Cyphocharax* is, in turn, hypothesized to be a synapomorphy for those taxa (SYNAPOMORPHY 75) (see also discussion immediately following).

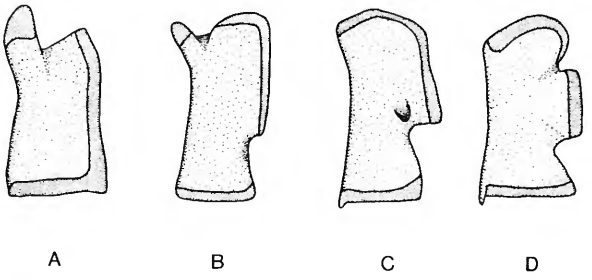

FIGURE 22.—Second hypobranchial: A, *Curimatopsis microlepis*, USNM 268867; B, *Potamorhina laticeps*, USNM 121325; C, *Psectrogaster amazonica*, USNM 261518; and D, *Pseudocurimata peruana*, USNM 285667. (Right side, dorsal view, anterior at top, lateral to left, dense patterned stippling represents cartilage.)

The continuous cartilage along the anterior border and anterior two-thirds of the medial margin of the second hypobranchial in that clade undergoes a secondary fission in the species of *Pseudocurimata*. In those taxa both the ossified and cartilaginous portions of the second hypobranchial proximate to the anterolateral margin of the third basibranchial are expanded vertically to form a more extensive articular surface (Figure 22D). Associated with that expansion is the separation of the continuous articular cartilage characteristic of proximate sister groups of *Pseudocurimata* into a broad anterior section and an elongate medial portion, with the two cartilages separated by an ossified region at the anteromedial angle of the bone. The expansion of the medial portion of the second hypobranchial and the subdivision of the originally continuous cartilage body along its anterior and medial margins are together considered a synapomorphy for the species of *Pseudocurimata* (SYNAPOMORPHY 101).

As noted above, a subdivided cartilage along the anterior and medial margins of the second hypobranchial also occurs in *Curimatopsis* and *Potamorhina*, in which that condition was hypothesized to be plesiomorphous. The forms of the cartilages on this element in *Curimatopsis* and *Potamorhina* on the one hand and *Pseudocurimata* on the other differ both in their relative locations and overall forms. The anterior cartilage in *Curimatopsis* and particularly *Potamorhina* is a small conical body limited to a process on the anterolateral corner of the bone. The anterior cartilage of *Pseudocurimata*, in contrast, is a narrow body extending over a broad portion of that margin of the bone. Similarly the gaps between the two cartilages are located in different regions in the two genera (compare Figure 22A,B with 22D). Futhermore the thickening characteristic of the second hypobranchial in *Pseudocurimata* species is absent in *Curimatopsis*. These morphological differences lead to a hypothesis of the non-homology of the two cartilage bodies on the anterior and medial margins of the second hypobranchial in *Curimatopsis* and *Potamorhina* versus *Pseudocurimata*, a hypothesis congruent with the overall most parsimonious scheme of relationships within the family (Figure 44).

Third Hypobranchial (H_3)

The third hypobranchial in characiforms is typically a flattened ossification that is unelaborated ventrally. The bone slants anteroventrally lateral to the third basibranchial, and terminates anteriorly in a rounded to distinctly acute triangular point. The anterior terminus of the third hypobranchial, be it an oblique point or an acute angle, serves as the point of attachment for a ligament that extends to the posteromedial surface of the second hypobranchial. The just described hypothesized plesiomorphous condition of the third hypobranchial is notably modified in all species of the Curimatidae. The members of the family have the anteroventral portion of the third hypobranchial elaborated into a discrete ventral process bearing both anterior and posterior extensions (AE and PE; Figures 23, 24). These elaborations, which lie in the connective tissue complex which parallels the walls of the ventral aorta, are not typical for characiforms and are hypothesized to be synapomorphous for the members of the Curimatidae (SYNAPOMORPHY 18).

Members of the family Hemiodontidae (*Anodus, Hemiodus, Hemiodopsis* (Vari, 1982a:19), *Micromischodus, Bivibranchia* [including *Atomaster,* Vari, 1985:512], and *Argonectes*) and one genus in the Chilodontidae (*Caenotropus labyrinthicus*) have the anterior portion of H_3 more developed ventrally than is the case in most characiforms. As a consequence the overall morphology of the anterior section of H_3 in those taxa is somewhat reminiscent of the anterior portion of the ventral H_3 complex of curimatids. Furthermore, two of the taxa, *Anodus* and *Caenotropus labyrinthicus,* also have the vertical flanges on the ventral surface of the third hypobranchial expanded in the connective tissue next to the walls of the ventral aorta, conditions similar to those characteristic of curimatids. The ventral elaborations and flanges in these genera differ from the similar processes in curimatids in a number of attributes. The ligament connecting the second and third hypobranchials in the Hemiodontidae and *Caenotropus* arises from the anterior tip of the anterior process of the third hypobranchial. That association of the ligament with that portion of the process is congruent with the hypothesis that the point of attachment, the elongate anterior point, in those taxa carried the H_2-H_3 ligament forward with it during its phylogenetic expansion anteriorly. Thus the lengthened anterior process of hemiodontids and *Caenotropus* is a consequence of the greater development of the entire ventral section of the third hypobranchial. In the Curimatidae, in contrast, the ligament attaches to the dorsal surface of the ventral process of the third hypobranchial proximate to the main body of that element (IL, Figures 23 and 24). The anterior projection of the ventral process, in turn, extends anteriorly distinctly ventral of the point of attachment of the ligament on the third hypobranchial. Thus it appears that the elongate anterior portion of the bone in the Curimatidae represents an anterior outgrowth of that portion of the bone ventral of the point of attachment of the ligament rather than an elongation of the entire element as is the case in the Hemiodontidae and *Caenotropus.*

The cited hemiodontids and chilodontids also differ from curimatids in the absence of any posterior extension on the ventral processes of H_3. Those differences in the details of the ventral process of H_3 and the overall most parsimonious hypothesis of phylogenetic relationships of the Curimatidae to characiform outgroups (Vari, 1983) lead to a hypothesis that the restructuring of the ventral surface of the third hypobranchial in the Curimatidae is a synapomorphy for that family, achieved in a different fashion in the Hemiodontidae and one genus in the Chilodontidae.

The area of attachment on the third hypobranchial for the ligament that extends between that element and the second hypobranchial (H_2) is modified in all *Steindachnerina* species.

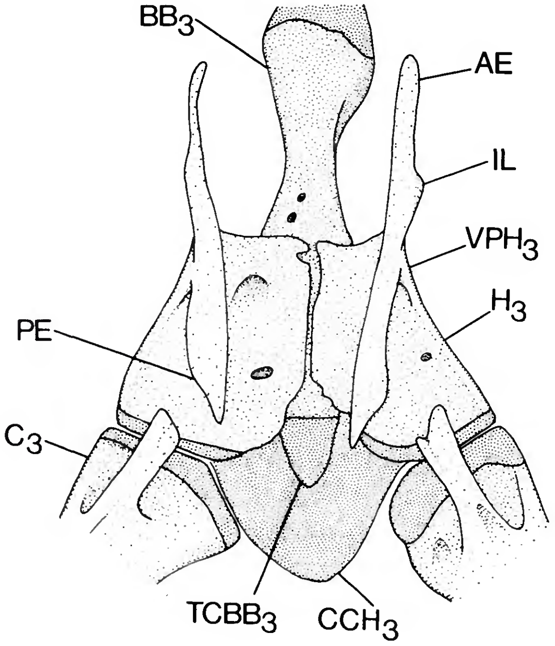

FIGURE 23.—*Curimata cyprinoides,* USNM 267964, third basibranchial, third hypobranchial, and anterior portion of third ceratobranchials, ventral view, anterior at top (dense patterned stippling represents cartilage).

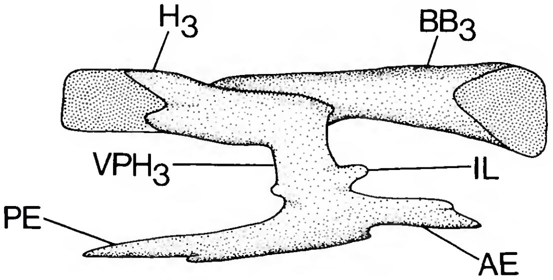

FIGURE 24.—*Steindachnerina hypostoma,* USNM 167802, third basibranchial and third hypobranchial, right side, lateral view, anterior to right (dense patterned stippling represents cartilage).

The connective tissue band between H_2 and H_3 typically attaches to the unelaborated anterolateral surface of the vertical strut of the ventral process of the third hypobranchial, or attaches to a slightly developed process in that area. In *Steindachnerina* species the point of attachment of the ligament on H_3 is rather a distinct process on the anterolateral surface of the ventral process. This condition is hypothesized to be derived given the absence of such a process in examined characiform outgroups and other lineages in the Curimatidae (IL, Figure 24) (SYNAPOMORPHY 99).

Third Ceratobranchial (C_3)

The third ceratobranchial of outgroups to the Curimatidae, including the Prochilodontidae has its dorsal margin transversely rounded or bearing a slight middorsal ridge extending along the longitudinal axis of the bone. A discrete longitudinal ridge along the dorsal surface of the bone characterizes all *Psectrogaster* species (SYNAPOMORPHY 92). Within *Curimata* a comparable ridge along the dorsal surface of C_3 also occurs in various nominal species (*mivartii, aspera, simulata, cerasina, alleni*, and two undescribed species) but differs in its shorter longitudinal extent along the bone. The ridge in those *Curimata* species also has a distinctly convex dorsal margin which contrasts with the straight edge of the ridge in *Psectrogaster*. The presence of a ridge, the derived condition, is considered to have arisen independently in *Psectrogaster* and some *Curimata* species within the context of the overall intrafamilial phylogeny arrived at in this study, and in light of the cited morphological differences.

Fourth Basibranchial (BB_4)

The fourth basibranchial in curimatids is a laterally compressed cartilaginous body without any associated toothplate along its dorsal surface. Only one modification of that element is pertinent to the current hypothesis of generic level relationships within the Curimatidae. In *Potamorhina* the gill arches are relatively elongate, an overall reconfiguration that is particularly produced in the fourth basibranchial. In all members of *Potamorhina* the fourth basibranchial occupies approximately two-thirds of the longitudinal extent of the branchial basket (Figure 25), an apomorphous lengthening over the condition in other curimatids and a synapomorphy for the genus (SYNAPOMORPHY 66) (see also Vari, 1984a:5 for a discussion of this character).

Fourth Ceratobranchial (C_4)

Outgroup comparisons reveal that the typical characiform fourth ceratobranchial although convex in cross section is unelaborated on its upper surface. All curimatids have various elaborations of the dorsal surface of the element relative to the hypothesized simple primitive condition. The species of *Curimatopsis* species have two distinct ridges running along the dorsomedial and dorsolateral margins of the bone (MR and LR, Figure 26A). These ridges extend from the wider anterior portion of the bone posteriorly along the main shaft of C_4, diverging somewhat posteriorly and are separated by a distinct longitudinal trough. The genera *Potamorhina, Curimata, Psectrogaster, Steindachnerina, Pseudocurimata, Curimatella*, and *Cyphocharax*, in contrast, have the ridges on the dorsal surface of the fourth ceratobranchial diverging to some degree anteriorly rather than being parallel in that region (Figure 26B,C). The ridges in those taxa are also positioned more towards the medial and lateral margins of the bone than in *Curimatopsis* (compare Figure 26A with 26B,C). The anterior ridge in these genera is furthermore more horizontally aligned than in *Curimatopsis*, a shift which results in a discrete bony pocket along the posteromedial surface of the bone. The lateral ridge in non-*Curimatopsis* curimatids, in turn, is rotated

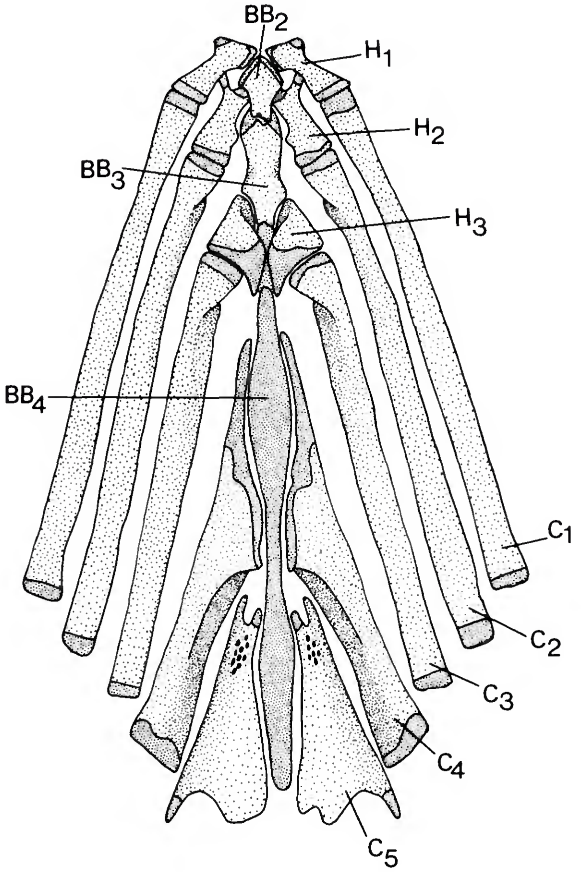

FIGURE 25.—*Potamorhina squamoralevis*, USNM 243228, ventral portion of gill arches, dorsal view, anterior at top (dense patterned stippling represents cartilage).

somewhat (Figure 26B) to distinctly lateral (Figure 26C). The presence of the ridges in one of these configurations, a character complex not present in examined characiform outgroups, is considered a synapomorphy for the species of the Curimatidae (SYNAPOMORPHY 28).

It is not possible to determine whether the parallel nearly vertical ridges along the dorsal surface of the fourth ceratobranchial, of *Curimatopsis* are derived, or whether the divergent, more horizontal processes characteristic of the other genera of the family are rather apomorphous. The unique nature of these processes in the Curimatidae among examined characiforms renders outgroup information useless in polarizing the transition series between the different states. Available ontogenetic data is similarly uninformative as to which state is derived. Finally the phyletic distribution of the two character states within the arrived at phylogeny is such that both the hypothesis that the *Curimatopsis* condition is derived and the alternative hypothesis that the ridge morphology in that genus is primitive are congruent with the final proposed scheme of relationships.

The ventral portion of the fourth ceratobranchial also demonstrates some phylogenetically significant variation within the Curimatidae. That portion of the bone is unelaborated in most characiform outgroups. In the Curimatidae and Prochilodontidae, in contrast, there is a distinct process arising from the medial margin of the ventral surface of the element, an elaboration which serves as the point of attachment for various connective tissue bands (Vari, 1983:13) (SYNAPOMORPHY 8). The degree of development of this process varies drastically within the Curimatidae. Some taxa (*Curimatopsis, Steindachnerina, Pseudocurimata, Curimatella,* and *Cyphocharax*) have small to very small processes on the ventral surface of the fourth ceratobranchial, whereas the genera *Potamorhina, Curimata,* and *Psectrogaster* have large, distinctly anteriorly directed processes on that element. The distribution of the enlarged processes, the presence of which is considered derived in light of the smaller processes in the Prochilodontidae and in other genera of the Curimatidae, is incongruent with the present phylogeny. Within the context of the phylogeny proposed herein (see "Synapomorphy List and Phylogenetic Reconstruction") it is most parsimonious to consider the acquisition of an enlarged process on the fourth ceratobranchial a synapomorphy for the clade formed by all curimatids other than *Curimatopsis* (SYNAPOMORPHY 57), with the absence of an enlarged process in *Steindachnerina, Pseudocurimata, Curimatella,* and *Cyphocharax* considered an apomorphous secondary loss (SYNAPOMORPHY 93). The alternative and next simplest hypothesis of the independent gain of an enlarged process in each of *Potamorhina, Curimata,* and *Psectrogaster* involves three ad hoc hypotheses.

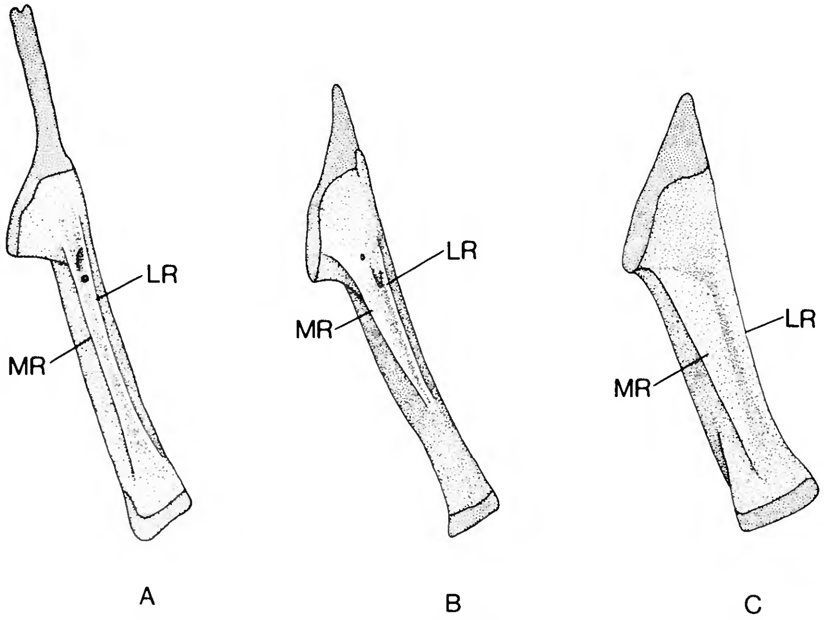

FIGURE 26.—Fourth ceratobranchial (C_4): A, *Curimatopsis microlepis*, USNM 268867; B, *Psectrogaster ciliata*, USNM 269990; C, *Curimata cyprinoides*, USNM 267964. (Right side, dorsal view, anterior at top, lateral to right, dense patterned stippling represents cartilage.)

Fifth Ceratobranchial (C_5)

The fifth ceratobranchial of most characiforms has a lateral shaft that terminates anteriorly in a cartilage-capped process lying proximate to the fourth basibranchial. Posteriorly that shaft ends in a cartilage at the posterolateral corner of the bone. Along the medial surface of that strut is a flattened plate that typically has a patch of small conical teeth on its dorsal surface. Such a form of C_5 is common to a variety of members of the New and Old World Characidae (e.g., *Brycon*, Weitzman, 1962, fig. 11), the Hemiodontidae (Roberts, 1974, fig. 32), Lebiasinidae (Weitzman, 1964, fig. 8), Erythrinidae (Roberts, 1969, fig. 35), Hepsetidae (Roberts, 1969, fig. 33), and other characiforms. As noted by Vari (1983:13), the fifth ceratobranchial of the Curimatidae and Prochilodontidae is distinctive in the significant degree of reduction or total absence of dentition on the dorsal surface of the ossification (SYNAPOMORPHY 7).

Although prochilodontids lack pharyngeal teeth on the ventral portions of the gill arches, they nonetheless retain the overall form of the fifth ceratobranchial generalized for characiforms that was just described (Figure 27A). All lineages in the Curimatidae differ from the phylogenetically widespread type of fifth ceratobranchial found in the Prochilodontidae in several respects. Members of the Curimatidae have a dorsally convex medial portion surface of the fifth ceratobranchial contrary to the flattened, although lateroventrally slanted form of the bone in examined outgroups (SYNAPOMORPHY 29). An additional derived character is the overall transverse expansion of the fifth ceratobranchial. That expansion has two components, firstly the widening of the bone medial to the portion of the bone delimited by the line extending between the anterior and posterolateral cartilage caps on the element, and secondly the further development of the ossification lateral to that line (Figure 27B,C). The transverse expansion of the fifth ceratobranchial is an additional synapomorphy for the members of the Curimatidae (SYNAPOMORPHY 30).

BUCCOPHARYNGEAL COMPLEX

The fleshy lining of the buccopharyngeal region in characiforms typically consists of a relatively smooth soft tissue layer conforming to the underlying convex inner surface of the oral cavity. Such a form of the roof of the mouth is characteristic of the Prochilodontidae and within the Curimatidae is also found in the species of *Curimatopsis* and *Potamorhina*. The genera *Curimata, Psectrogaster, Steindachnerina, Pseudocurimata, Curimatella,* and *Cyphocharax* have the soft tissue layers of the buccopharyngeal region elaborated to various degrees (SYNAPOMORPHY 76). Collectively these modifications, irrespective of degree of development, are referred to herein as the buccopharyngeal complex.

The simplest form of the elaboration consists of three longitudinally oriented folds on the roof of the mouth: a median fold and a pair of lateral folds. These soft tissue folds begin somewhat behind the oral valve and terminate distinctly anterior of the dorsal portions of the gill arches. Such a relatively simple morphological plan, characteristic of the majority of curimatids, is dramatically elaborated in two subunits of the family, the genus *Curimata* and the majority of species in *Steindachnerina*.

All *Curimata* species have the three primary mouth folds (MF and paired LF, Figure 28) typical of many curimatids expanded into large dangling flaps that extend ventrally from

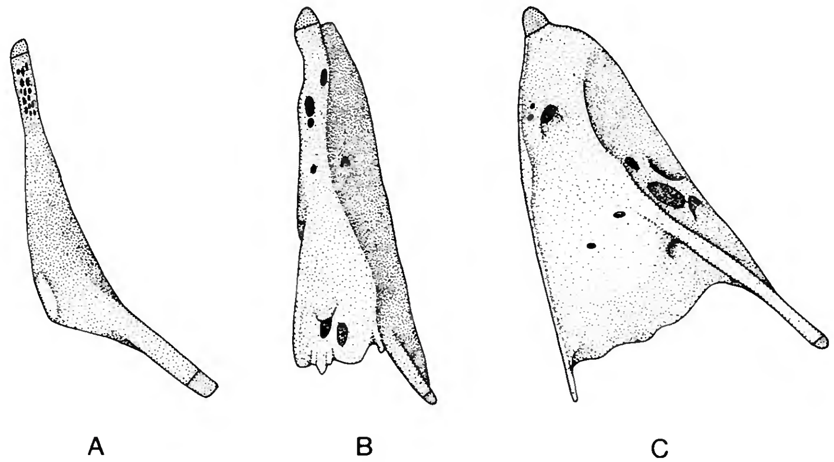

FIGURE 27.—Fifth ceratobranchial (C_5): A, *Prochilodus rubrotaeniatus*, USNM 225419; B, *Curimatopsis microlepis*, USNM 268867;, and C, *Curimata cyprinoides*, USNM 267964. (Right side, dorsal view, anterior at top, lateral to right, dense patterned stippling represents cartilage.)

the roof of the oral cavity. These flaps abut against the oral valve anteriorly and extend posteriorly midway to the anterior terminus of the dorsal portions of the gill arches (GA). An additional innovative feature of the buccopharyngeal complex in *Curimata* species is the series of secondary folds (SF) on the roof of the oral cavity. These secondary folds either arise from the margins of the primary folds, or if independent of those major flaps, are aligned parallel to them. The greater degree of development of the median and lateral folds and the occurrence of secondary folds in the *Curimata* buccopharyngeal complex are considered derived in light of their unique nature within examined characiforms and synapomorphous for the genus (SYNAPOMORPHY 82).

The second significant elaboration of the soft tissues of the roof of the mouth within the Curimatidae involves the lobulate form of the buccopharyngeal complex characteristic of most species in *Steindachnerina*. All nominal members of the genus, except *S. bimaculata*, *S. semiornata*, *S. trachysteta*, *S. bimaculata sialis*, *S. pterostrigma*, *S. melanira*, *S. conspersa*, *S. leucisca leucisca*, *S. leucisca bolivae*, *S. argentea*, and *S. binotata*, have numerous lobulate protruberances extending ventrally from the roof of the mouth (ALP, Figure 29). These processes, which totally fill the entire anterior portion of the roof of the oral cavity, undergo an ontogenetic elaboration from relatively simple, discrete finger-like projections, to well developed, thickly packed lobulate structures. The *Steindachnerina* species with such complex protruberances also have in common elaborate lobed pads (PLP) to each side of the rear of the buccal cavity in the region between the rear of the anterior lobulate processes and the forward limit of the dorsal portion of the gill arches (GA, Figure 29). Those structures are not developed to a comparable degree in species of *Curimata* or in curimatids with less elaborate forms of the anterior portion of the buccopharyngeal complex.

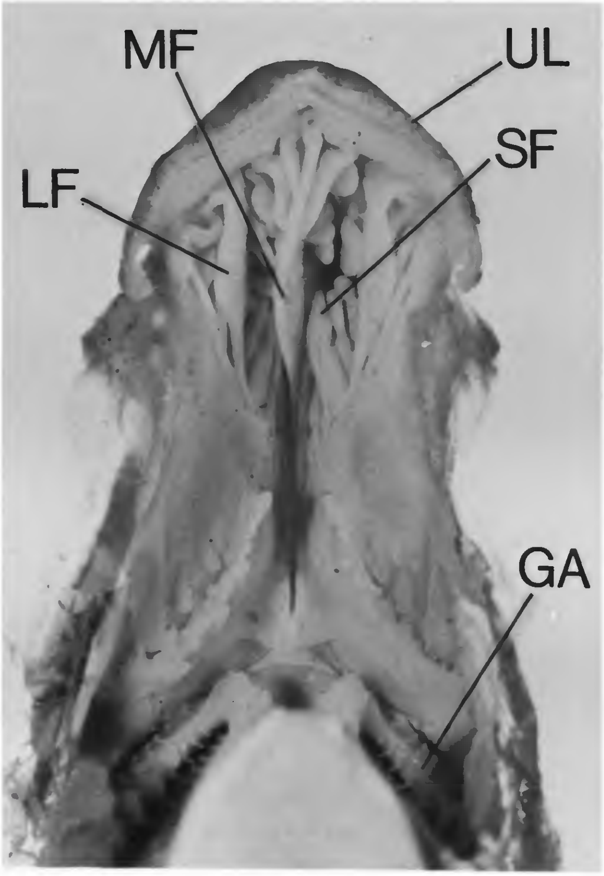

FIGURE 28.—Roof of the buccopharyngeal chamber and anterior portion of gill arches of *Curimata cyprinoides*, USNM 267963, ventral view showing buccopharyngeal complex (hyoid apparatus, ventral portion of gill arches, eyes, and associated tissues removed).

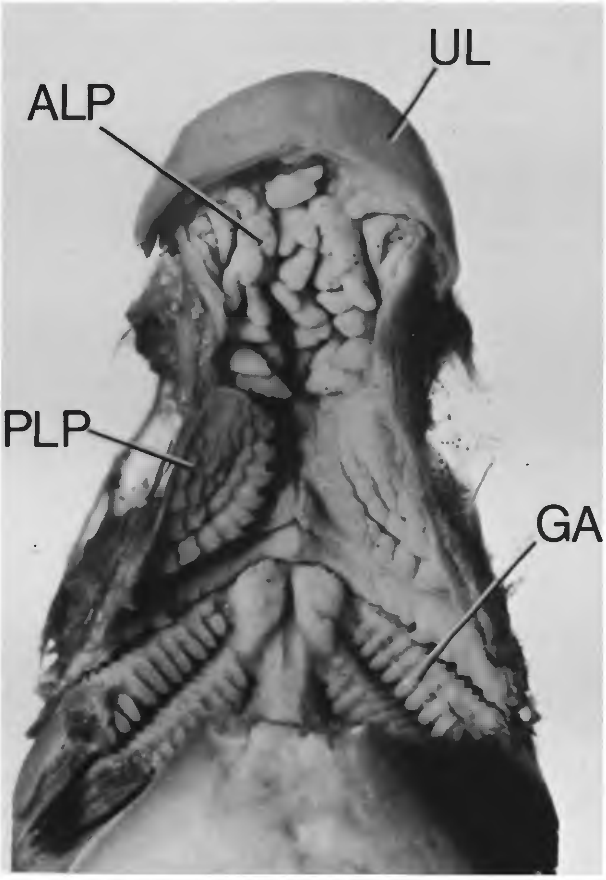

FIGURE 29.—Roof of the buccopharyngeal chamber and anterior portion of gill arches of *Steindachnerina hypostoma*, USNM 261493, ventral view showing buccopharyngeal complex (hyoid apparatus, ventral portion of gill arches, eyes, and associated tissues removed).

The dangling lobulate processes in most *Steindachnerina* species differ significantly in position and detail from the longitudinal folds characteristic of *Curimata*. The hypothesis of homoplasy predicated on the basis of these morphological differences is also congruent with the most parsimonious hypothesis of relationships within the Curimatidae. That phylogenetic scheme indicates that *Curimata* and the subunit of *Steindachnerina* with buccopharyngeal complex elaborations do not constitute a monophyletic lineage, and that the increased development of the complex in the two lineages was consequently achieved independently.

The various types of buccopharyngeal complex, be they the simple three folds of many curimatid species or the more developed modifications just described for *Curimata* and most *Steindachnerina* species, all serve to increase the surface area of the dorsal surface of the buccal cavity. The buccal region of teleosts is well endowed with mucus-secreting cells (see Kapoor and Evans, 1975) and histological examinations of the foldings and lobulate bodies in curimatids with well developed buccopharyngeal complexes shows that the surfaces of these processes are profusely endowed with mucus-secreting cells (MPL, Figures 30, 31). Thus the majority of curimatids, in particular the species of *Curimata* and most species of *Steindachnerina*, presumably have a pronounced increase in their ability to generate mucus in the buccal cavity, an adaptation perhaps correlated with their specialized microphagous and detritivorous diet.

The more elaborate forms of the buccopharyngeal complex in curimatids are similar to the vomero-palatine organs of some groups of Old World cyprinids recently discussed by Reid (1982). Although Old World cyprinids and curimatids are not closely related, they do have in common a microphagous feeding habit. Reid, refining and further developing a concept suggested by Matthes (1963), hypothesized that the vomero-palatine organ in Old World cyprinids functioned in bolus-formation. He proposed that the buccopharyngeal modifications served in the production of relatively large amounts of mucus, and in the mixing of such precipitating mucus with ingested particles, particularly *aufwuchs* (a conglomerate of algae, minute animals, detritus and inorganic matter). Field observations have shown that curimatids pick at the *aufwuchs* which coats many subaquatic surfaces in Neotropical freshwaters, both running and still (pers. observ.). The utilization of that food source by at least some curimatids is also indicated by the food item studies of various authors (Azevedo et al., 1938; de Godoy, 1975; Nomura and Hayashi, 1980; Nomura and Taveira, 1979). Thus Reid's hypothesis of a particle-precipitating mucus system in some Old World Ostariophysan groups is apparently also applicable to the Curimatidae, paralleling the system used by some microphytophagous cichlid fishes (Moriarty et al., 1973) and some anuran tadpoles (Wasserzug, 1972).

HYOID ARCH

Urohyal

The four branchiostegal rays of each side of the head in conjunction with their associated musculature and branchiostegal membranes are an interconnected complex that forms the ventral limits of the buccal cavity. In many, if not most, characiforms the branchiostegal rays and associated soft parts of each side of the head form a flexible complex that is separate (sensu McAllister, 1968) from its counterpart of the opposite side. The degree of separation of the complexes of each side varies among taxa in the order, but in many groups, particularly those with predatory or omnivorous habits, the opening extends

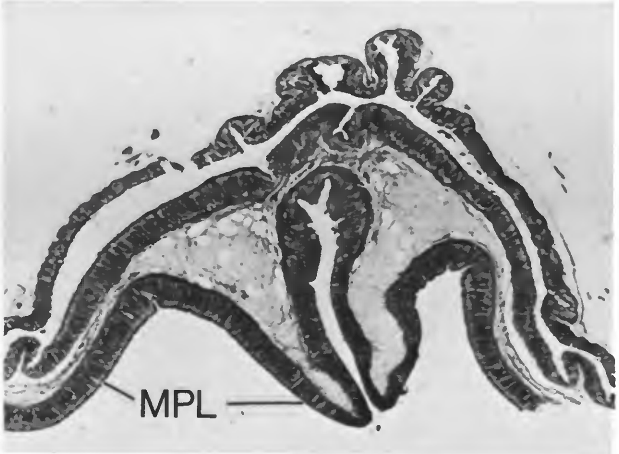

FIGURE 30.—Histological section through flaps of buccopharyngeal complex of *Curimata cyprinoides*, USNM 267963.

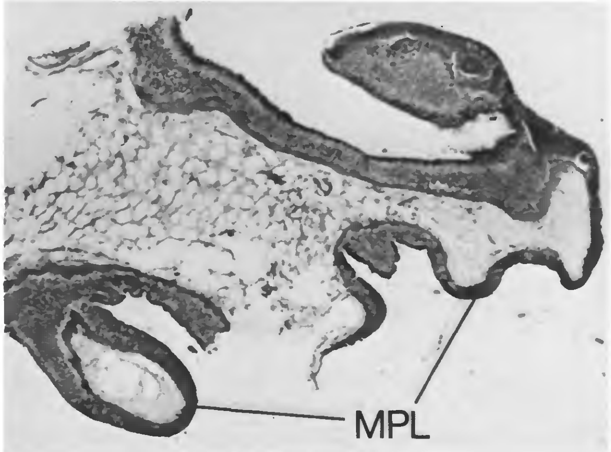

FIGURE 31.—Histological section through lobes of buccopharyngeal complex of *Steindachnerina hypostoma*, USNM 261513.

far anteriorly resulting in an elongate gill aperture on each side. The condition in the Curimatidae differs from that generalized bauplan in having a broad connection of the branchiostegal rays of each side across the ventral midline to the contralateral complex, and with an attachment of the rays medially to the urohyal. These interconnections result in a dramatic decrease in the relative size of the aperture of the gill openings on each side of the head, and in the degree of mobility in the entire branchiostegal complex.

A broad contact between the branchiostegal ray complexes of each side comparable to that in the Curimatidae is also found in the families Prochilodontidae, Anostomidae, and Chilodontidae, which are the closest relatives of the Curimatidae. Such an extensive attachment of the complex also occurs in some characiform outgroups including the Neotropical Parodontidae and subunits of the Old World family Distichodontidae. The alterations of the hyohyoidei abductores muscles associated with the broad contact of the branchiostegal complexes of each side of the head to each other and to the urohyal, and the apomorphous nature of those modifications in the Curimatidae, Prochilodontidae, Anostomidae, and Chilodontidae were discussed by Vari (1983:45–46, fig. 40). Within that set of four families the form of the interconnection between the branchiostegals and urohyal in the species of the Curimatidae is unique in the presence of a distinctive highly developed midventral ligament (Figure 32). That ligament (MVL) is enclosed within the connective tissue complex joining the medial branchiostegal rays (BR) of the two sides and consists of a central cord-like section with anterior and posterior medially divided segments. The anterior branch of the ligament of each side is rounded in cross-section and arises from a relatively broad area on the ventral surface of the ventral hypohyal (VH). Posteriorly the central cord-like ligament subdivides into lateral band-like portions that extend along the posterior margins of the branchiostegal rays and progressively becomes thinner posteriorly. Although the medial ligamentous complex is also found in the families Chilodontidae, Anostomidae, and Prochilodontidae, it is much less well defined and not as well developed as the condition in the Curimatidae. Thus the condition in the last family is considered derived.

The central median cord-like portion of the described ligamentous complex extends along a distinct groove located along the ventromedial surface of the urohyal. That urohyal groove is delimited by ventrolaterally aligned flanges extending from the lower margin of the main body of that ossification. The Prochilodontidae, the sister group to the Curimatidae, and the Anostomidae and Chilodontidae, which together form the sister group to the curimatid-prochilodontid clade, both have the ventral portions of the urohyal expanded laterally to differing degrees; however, in all these families the bone is ventrally flattened, rather than having a central groove. Furthermore the lateral flanges in those proximate outgroups are not ventrolaterally oriented. Thus neither the highly developed ligamentous system along the midline of the branchiostegal complexes, nor the groove on the ventral surface of the urohyal are known to occur in characiforms outside of the Curimatidae. The complex formed by the midventral ligament and the urohyal is consequently hypothesized to be a synapomorphy for the members of the Curimatidae (SYNAPOMORPHY 31).

The form of the urohyal is quite variable within the Curimatidae, both in terms of overall morphology and in various details. The continuum between most different morphological states makes it difficult, if not impossible, to non-arbitrarily delimit much of that variability in terms of discrete characters applicable to a phylogenetic analysis. Several distinct character states exist which are, however, useful in generating a hypothesis of generic level relationships.

As noted above, the urohyal of the Curimatidae is characterized by a posteroventrally angled flange along both sides of its ventral margin. In cross section the bone consequently has the form of an inverted "Y"; the ventral arms of which vary in the degree of lateral development within the family. In *Curimatopsis* the ventrolateral flanges are quite narrow along their entire length, whereas in the other lineages

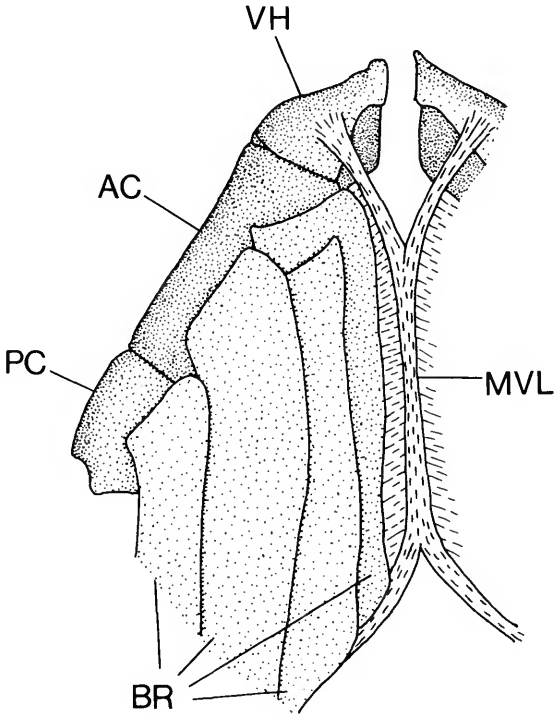

FIGURE 32.—*Cyphocharax abramoides*, USNM 267953, hyoid arch, anterior portion of branchiostegal rays and midventral ligament (medial portion and right side, ventral view, anterior at top, basihyal not illustrated, halves of arch separated laterally from normal positions).

of the Curimatidae, the flanges are wider, sometimes considerably so, particularly anteriorly. Outgroup comparisons reveal wide flanges on the urohyal in the Prochilodontidae, the sister group to the Curimatidae. The sister clade to the lineage formed by those two families shows two divergent conditions; narrow flanges in the Anostomidae and wide processes in the Chilodontidae. The condition in the immediate outgroup, the Prochilodontidae, together with parsimony considerations in the broader outgroup, including the Anostomidae and Chilodontidae, support the hypothesis that a urohyal with wide ventrolateral flanges is primitive for the family Curimatidae. Thus the narrow processes in the species of *Curimatopsis* is considered a reductive feature that is synapomorphous for the members of that genus (SYNAPOMORPHY 45).

The urohyal in the Prochilodontidae, Anostomidae, and Chilodontidae are all relatively short longitudinally with their ventral portions terminating approximately at the point where the medialmost branchiostegal rays diverge laterally. The Curimatidae, in contrast, has the ventral portions of the urohyal extending moderately to distinctly beyond that point, a condition that is thus considered a synapomorphy for the members of the family (SYNAPOMORPHY 32).

Within the Curimatidae, the genera *Curimatopsis, Potamorhina,* and *Psectrogaster* all have a urohyal that is distinctly elongate, with one-third to one-half of the ossification extending beyond the rear of the point of the lateral divergence of the medial branchiostegal rays. Such a degree of posterior development of the urohyal is not found in the remainder of the family, and is considered derived on the basis of outgroup comparisons. The possession of an elongate urohyal does not, however, delimit a monophyletic subunit of the family in the final proposed intrafamilial phylogeny. Within that phyletic scheme (Figure 44), *Curimatopsis* and *Potamorhina* are sequential clades but are separated from *Psectrogaster* by the lineage consisting of *Curimata.* The sister group to *Psectrogaster,* the assemblage consisting of *Steindachnerina, Pseudocurimata, Curimatella,* and *Cyphocharax* is characterized by short urohyals. Three equally parsimonious hypotheses exist to explain the distribution of the derived condition, the elongate urohyal, within the Curimatidae. First, there may have been independent acquisition of the modification in the three lineages, *Curimatopsis, Potamorhina,* and *Psectrogaster.* Second, there may have been a single synapomorphic acquisition at the base of the Curimatidae, with secondary shortening of the urohyal occurring independently in *Curimata* on the one hand and the assemblage consisting of *Steindachnerina, Pseudocurimata, Curimatella,* and *Cyphocharax* on the other. Finally, the elongation may have been acquired at the level of Curimatidae, with a secondary shortening occurring in the clade consisting of *Curimata, Psectrogaster, Steindachnerina, Pseudocurimata, Curimatella,* and *Cyphocharax,* with a secondary lengthening in *Psectrogaster.*

Each of these hypotheses involves three ad hoc hypotheses about evolutionary events. Given these equally parsimonious alternatives, it was not possible to determine the appropriate phylogenetic levels at which to use these characters as synapomorphies; consequently, they are not incorporated in the cladogram (Figure 44), although the feature was included in the PAUP analysis and has been assigned a synapomorphy number (SYNAPOMORPHY 105) for analysis and discussion purposes.

Basihyal (BH) and Basihyal Tooth Plate (BHTP)

The basihyal is an unpaired median element that extends anteriorly from between the paired dorsal hypohyals. The element typically consists of a cartilaginous core, at least in juveniles, enveloped posteriorly and to varying degrees anteriorly by a sheath of bone. Along its dorsal surface the basihyal may or may not be partially covered by an independent ossification, the thin basihyal tooth plate, that extends anteriorly over the dorsal surface of the cartilaginous portion of the element (Figure 33B). Although the form of the complex formed by the basihyal and basihyal tooth plate varies considerably within the family, the continuum between the majority of morphological states permits the delimitation of only one evidently derived character state.

The majority of curimatids have an elongate to elongate triangular basihyal complex with relatively straight lateral margins (Figure 33A). In *Steindachnerina* species, rather, the bone-cartilage complex is apomorphously laterally expanded anteriorly, with the anterior cartilaginous portion notably flared outwards. Associated with this reconfiguration of the basihyal is a comparable lateral expansion of the basihyal tooth plate (BHTP, Figure 33B). The anterior expansion of the basihyal and basihyal tooth plate are apomorphous for the species *Steindachnerina* (SYNAPOMORPHY 100). A similarly expanded basihyal-basihyal tooth plate complex also occurs in the

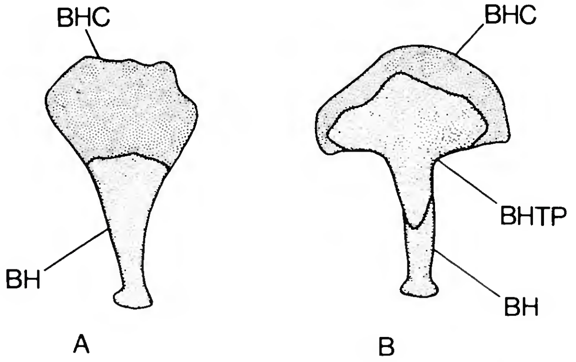

FIGURE 33.—A, Basihyal of *Potamorhina altamazonica,* USNM 257367; B, basihyal and basihyal tooth-plate of *Steindachnerina bimaculata,* USNM 261450. (Dorsal view, anterior at top, dense patterned stippling represents cartilage.)

Prochilodontidae, the sister group to the Curimatidae. In light of the unique nature of the *Steindachnerina* form of the basihyal complex within the Curimatidae and the topology of the most parsimonious phylogenetic scheme in that family (Figure 44), the hypothesis that the expansion of the basihyal and its associated tooth plate in the Prochilodontidae and *Steindachnerina* represent homoplasies is the most parsimonious.

A basihyal tooth plate is present in the Anostomidae (see Winterbottom, 1980, fig. 45), Prochilodontidae (see Vari, 1983, fig. 22) and Chilodontidae (see Vari, 1983, fig. 24), the immediate sister groups to the Curimatidae. Within the Curimatidae the ossification is variously present at the generic and subgeneric level. Although lacking in *Curimatopsis, Potamorhina,* and *Psectrogaster,* that element is found in a minority of *Curimata* species and in the large majority of the species of *Steindachnerina, Pseudocurimata, Curimatella,* and *Cyphocharax*. It would thus appear that the primitive condition within the family is for the ossification to be absent. The presence of a basihyal tooth plate in most members of *Steindachnerina, Pseudocurimata, Curimatella,* and *Cyphocharax* is thus considered to be indicative of the monophyly of that assemblage, (Synapomorphy 94) albeit with qualifications due to the absence of the tooth plate in some members of that lineage.

Branchiostegal Rays (BR_{1-4})

The Curimatidae, Prochilodontidae, Chilodontidae,and Anostomidae all typically have four branchiostegal rays, although that number is reduced to three in some anostomids (Winterbottom, 1980). The condition in the prochilodontid *Semaprochilodus laticeps* (Figure 34A) is representative of the generalized condition of the portions of those elements proximate to the hyoid arch in that family. That morphological plan also represents the plesiomorphous condition of those portions of the branchiostegal rays for the Chilodontidae and Anostomidae with respect to the characters of interest in this discussion.

The first two branchiostegal rays in the Prochilodontidae (BR_1 and BR_2) attach to a depression on the ventral surface of the anterior ceratohyal. According to the degree of ossification of the entire hyoid arch, a largely size related function, the area of attachment either has the form of two ossified notches (Figure 34A) or is a broader concave region subdivided by smaller cartilages (Figure 34B). Anterodorsally the margins of the first two branchiostegal rays (BR_1 and BR_2) are slightly convex or straight, but without any pronounced angle proximate to the point of articulation. The third branchiostegal ray (BR_3) attaches to the posterolateral surface of the anterior ceratohyal and only slightly overlaps the posterolateral margin of the second branchiostegal ray leaving the portion of that bone proximate to the anterior ceratohyal exposed laterally.

All members of the Curimatidae demonstrate several derived modifications of the branchiostegal rays that differ from the morphological plan just described. In the Curimatidae the anterodorsal portion of the first and second branchiostegals (BR_1 and BR_2) is dorsally expanded resulting in a pronounced angle in the anterior margin of those bones. As a consequence the margins of these ossifications are distinctly concave proximally, more so in the case of the first branchiostegal ray. The anterodorsal expansion of the proximate portion of the third branchiostegal (BR_3) of curimatids is even more pronounced. This expansion results in the third branchiostegal ray distinctly overlapping the dorsal portion of BR_2 laterally and completely covering the section of that element articulating with the anterior ceratohyal (Figure 34B). In light of the conditions in the proximate outgroups, these modifications of the portions of the first to third branchiostegal rays approximating the hyoid arch are considered apomorphous for the members of the Curimatidae (Synapomorphy 33).

Antorbital and Infraorbitals

The orbit in the vast majority of characiforms is ringed by a series of eight bones, an antorbital, a supraorbital, and six infraorbitals, with the infraorbitals bearing portions of the laterosensory canal system. Variations in the presence or

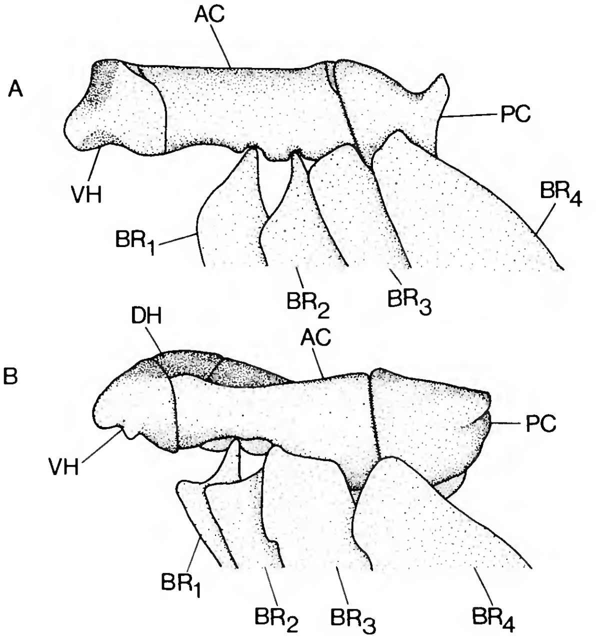

Figure 34.—Hyoid arch (without interhyal) and proximate portion of branchiostegal rays: A, *Semaprochilodus laticeps*, USNM 270239; and B, *Steindachnerina bimaculata*, USNM 261450. (Left side, lateral view, anterior to left, dense patterned stippling represents cartilage.)

absence of some of these elements, their relative sizes, and presence and form of the included laterosensory canal segments serve to define subunits of the Curimatidae.

Antorbital

The antorbital (the adnasal of Gregory, 1933, and Daget, 1964), an element lying immediately anterior to the ventral process of the lateral ethmoid, demonstrates only one phylogenetically significant character in the Curimatidae. As noted by Vari (1982a:8) the antorbital is absent in all species of *Curimatopsis*. The possibility that the absence of the antorbital in *Curimatopsis* is the result of some paedomorphic process would in first consideration appear likely in light of the relatively small adult size of most species of *Curimatopsis*. Such an explanation also seems applicable in the case of the diminutive African characid *Lepidarchus adonis* Roberts which also lacks an antorbital (Roberts, 1966). In *Curimatopsis*, however, the ossification is absent not only in the diminutive members of the genus such as *C. evelynae*, but even in a 75.8 mm SL specimen of *C. microlepis* (USNM 268867) cleared and counterstained for cartilage and bone. Thus the absence of the bone in all *Curimatopsis* species does not appear to simply represent a paedomorphic feature. Weitzman and Vari (1988) noted that paedomorphosis must be analyzed within a phylogenetic context in which miniaturization and miniatures are evaluated relative to the size and features of those taxa phylogenetically proximate to the potential miniatures. Relative to the much larger body sizes of the Prochilodontidae, and the immediate sequential sister groups to *Curimatopsis* in the Curimatidae, even the largest *Curimatopsis* species is of a reduced overall size. Regardless of the underlying cause, the lack of an antorbital is considered a synapomorphy for *Curimatopsis* species (SYNAPOMORPHY 41).

First Infraorbital (IO_1)

The first infraorbital, the most anterior of that series of bones ringing the ventral and posterior portions of the orbit typically has a discrete tube-like laterosensory canal segment in Characiformes. Within the Curimatidae, a laterosensory canal segment in the first infraorbital is present in the vast majority of species, but is absent in the five species of *Curimatopsis*, four species of *Cyphocharax* (*gillii, saladensis, punctata, vanderi*), and a single species in *Steindachnerina* (*binotata*). On the basis of the overall phylogeny, the lack of a laterosensory canal segment in the first infraorbital is considered a synapomorphy that arose independently in *Curimatopsis* on the one hand (SYNAPOMORPHY 46) and the cited species of *Cyphocharax* on the other, and which is an autapomorphy for *Steindachnerina binotata*.

Gregory and Conrad (1938, fig. 28) in their drawing of an unspecified "*Curimata*" species, illustrate a single canal bearing bone anterior of the lateral ethmoid (their prefrontal plus paraethmoid). That bone, which they identify as the lacrymal, is shown as extending from the supraorbital dorsally around the anterior and anteroventral margins of the orbital rim to the second infraorbital (their second suborbital) posteriorly. The illustrated lacrymal of those authors thus appears to actually represent a combination of two separate bones, the antorbital (that portion of their ossification proximate to the lateral ethmoid) and the first infraorbital (the ventral canal-bearing section of their illustration). Their illustration is also incorrect in showing the infraorbital series posterior of the first infraorbital as a single continuous ossification. In all examined curimatids the second through sixth infraorbitals are discrete elements.

Fourth and Fifth Infraorbitals (IO_4 and IO_5)

The fourth infraorbital commonly contains a tripartite canal in the near relatives of the Curimatidae, the Prochilodontidae (e.g., *Ichthyoelephas* Posada-Arango, Roberts, 1973, fig. 17), Anostomidae (e.g., *Synapotalaemus* Myers and Fernández-Yépez, Winterbottom, 1980, fig. 32) and Chilodontidae (e.g., *Caenotropus*, Géry, 1964b, fig.1). The primary canal segment in this element extends parallel to the anterior margin of the bone along the orbital rim and communicates dorsally and ventrally with comparable canal segments in the fifth and third infraorbitals respectively. The fourth infraorbital also has a horizontal or slightly posteroventrally inclined, posteriorly directed side branch (HC-IO_4) of the laterosensory canal segment. That canal extends posteriorly to the proximity of the opening in the preopercle into the preopercular laterosensory canal system, and sometimes communicates posteriorly with an unossified laterosensory canal segment in the tissue of the adipose eyelid overlying the opercle. The laterosensory canal segment of the fifth infraorbital continues along the arch of the canal segments in the third and fourth infraorbital, without any pronounced angle between the primary axes of the sensory canal segments in the fourth and fifth infraorbitals.

The pattern described above is most common in the Prochilodontidae, Anostomidae, and Chilodontidae, with differences among those families relative to this pattern involving features not pertinent to the Curimatidae. Among curimatids a morphological plan of the fourth and fifth infraorbitals comparable to that of the cited outgroups occurs in *Curimatopsis, Potamorhina, Curimata*, and *Psectrogaster* (Figure 35A,B). The genera *Steindachnerina, Pseudocurimata, Curimatella*, and *Cyphocharax*, in contrast, have the anterior canal segment of the fourth infraorbital (IO_4) more posteriorly angled, with an associated reduction or elimination of the posterior horizontal sidebranch in that bone (HC-IO_4, Figure 35C). The laterosensory canal segment in the fifth infraorbital (IO_5), in turn, is more distinctly angled posteroventrally than in the generalized characiform condition. Together, reorientations of these canals are most obvious in the distinct angle

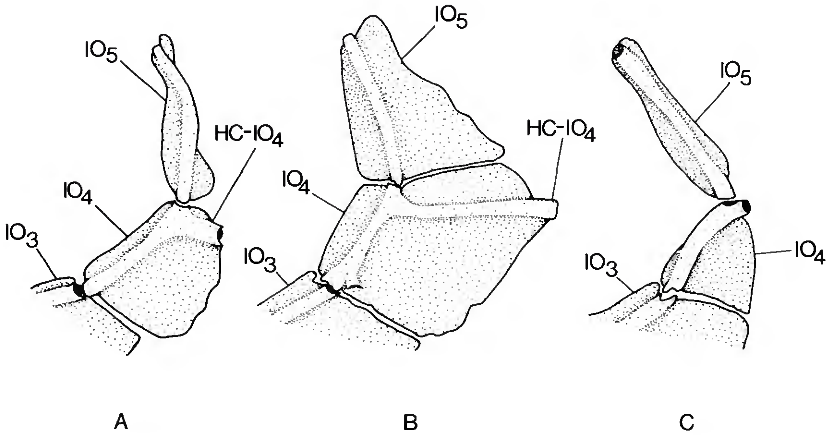

FIGURE 35.—Fourth and fifth infraorbital and dorsal portion of third infraorbital: A, *Psectrogaster curviventris*, USNM 243221; B, *Potamorhina altamazonica*, USNM 257367; and C, *Curimatella meyeri*, USNM 261508. (Left side, lateral view, anterior to left.)

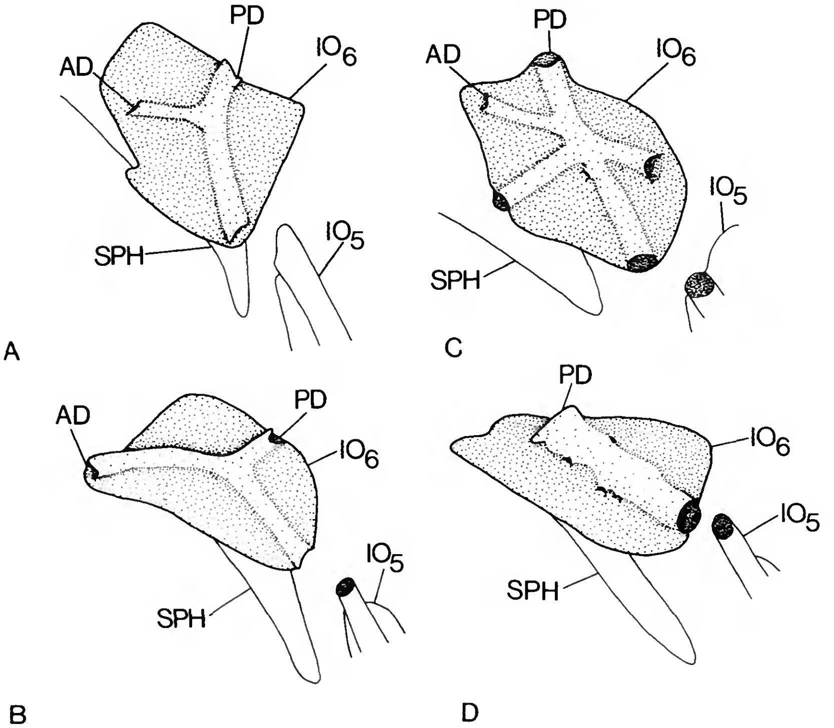

FIGURE 36.—Sixth infraorbital (dermosphenotic): A, *Psectrogaster amazonica*, USNM 261518; B, *Potamorhina altamazonica*, USNM 257367; C, *Curimata cyprinoides*, USNM 267964; and D, *Steindachnerina conspersa*, USNM 232224. (Left side, lateral view, anterior to left.)

between the primary axes of the laterosensory canal segments in the fourth and fifth infraorbitals; a condition which contrasts with the continuous arch of the canals in those elements in outgroups within (Figure 35A,B) and outside of the Curimatidae (SYNAPOMORPHY 95).

Most species of *Potamorhina* retain the plesiomorphous orientation of the fourth and fifth infraorbitals and their canals. The fourth and fifth infraorbitals in that genus are, however, unique within the Curimatidae in their pronounced posterior development. This is particularly the case for the fourth infraorbital and the horizontal laterosensory canal segment in that ossification, with these shifts in the relative positions of those canals considered together to be an apomorphy for the genus (SYNAPOMORPHY 45). *Potamorhina pristigaster,* which shares with its congeners the posterior expansion of the fourth infraorbital also has the form of the laterosensory canal segments in the fourth and fifth infraorbitals autapomorphously modified. That species has a distinct acute angle between the laterosensory canal segments in the fourth and fifth infraorbitals reminiscent of the condition in *Steindachnerina, Pseudocurimata, Curimatella,* and *Cyphocharax.* That decreased angle between the axes of the canals in these bones is a consequence of the posterior repositioning of the two ossifications relative to the orbital rim. The condition differs significantly from the reduced angle between the canal segments in *Steindachnerina, Pseudocurimata, Curimatella,* and *Cyphocharax* which results from the reorientation of the canal segments in the fourth and fifth infraorbitals which have not themselves been shifted posteriorly from the orbital rim in those taxa. Thus the *P. pristigaster* condition is considered an autapomorphy nonhomologous with the situation in *Steindachnerina, Pseudocurimata, Curimatella,* and *Cyphocharax.*

Sixth Infraorbital (IO_6)

The sixth infraorbital (the dermosphenotic of some authors) is an independent ossification that roofs over the dilatator fossa on the lateral surface of the neurocranium. The generalized condition of the ossification in characiforms has a tripartite laterosensory canal system comparable to that of Figure 36A,B, with the ventral arm of the complex contacting the laterosensory canal segment in the fifth infraorbital (IO_5). The posterodorsal branch of the IO_6 canal system (PD) approximates the anterior opening of the pterotic sensory canal, and the anterior branch extends anterodorsally to the frontal. Such a condition of the laterosensory canal system in the sixth infraorbital is the basic pattern in the Prochilodontidae, Anostomidae, and Chilodontidae, along with a variety of other characiforms including members of the Old World families Citharinidae (*Citharinus,* Daget, 1962a, fig, 7; *Citharidium* Boulenger, Daget, 1962b, fig. 10), Distichodontidae (*Xenocharax,* Daget, 1960, fig. 7; see also Vari, 1979:296–301 for the remainder of the family), Hepsetidae (Roberts, 1969, fig. 1), and Characidae (*Hydrocynus,* Allis, 1905, fig. 13). In the Neotropical realm a similar morphology of the sixth infraorbital is found in many, although not all, members of the Characidae (e.g., *Brycon,* Weitzman, 1962, figs. 8, 9), Hemiodontidae, and Erythrinidae (e.g., *Hoplias,* Roberts, 1969, fig. 3) among other families.

Several modifications of the sixth infraorbital and its enclosed laterosensory canal segment define subunits of the Curimatidae. The relative size of the sixth infraorbital is reduced in *Curimatopsis microlepis* and *C. macrolepis.* The three remaining species of the genus (*evelynae, crypticus,* and *myersi*) demonstrate no trace of an ossified sixth infraorbital. As adults these latter species are some of the smallest in the family and it is possible that the reduced sixth infraorbital represents a paedomorphic event characteristic of the clade. That possibility is particularly notable since the sixth infraorbital is absent in a number of diminutive characiforms (see Weitzman and Fink, 1983, fig. 24, and Weitzman and Fink, 1985:63, fig. 54). Nonetheless it is noteworthy that cleared and stained specimens of *Curimatopsis crypticus* of 42.1 mm SL show no indication of an ossified sixth infraorbital although the element is present in comparably sized individuals of other curimatid species that achieve larger adult body sizes. Regardless of the process underlying the lack of an ossified dermosphenotic in these taxa, that absence is considered derived and a synapomorphy for the clade consisting of *Curimatopsis evelynae, C. myersi,* and *C. crypticus* (*Curimatopsis* SYNAPOMORPHY F). Similarly the combination of a reduction or loss of that bone is hypothesized to be synapomorphous for the entire genus (SYNAPOMORPHY 42).

Within the Curimatidae, two clades at the generic and suprageneric levels are definable by derived states of the sixth infraorbital and its contained laterosensory canal segment. The elaboration of the plesiomorphous tripartite IO_6 laterosensory canal segment via the addition of a posteroventral and sometimes also anteriorly and anteroventrally aligned side branches (Figure 36C) was discussed by Vari (1984a:6). That condition, synapomorphous for the species of *Potamorhina* (SYNAPOMORPHY 67), is not analyzed again here.

Whereas a tripartite canal system in the sixth infraorbital or an elaboration of that pattern are common to species of *Curimatopsis* with that element, along with *Potamorhina, Curimata,* and *Psectrogaster,* all other curimatids have only a single unbranched laterosensory canal segment in that ossification (Figure 36D). That simplified straight canal segment communicates with the fifth infraorbital sensory canal (IO_5) ventrally, and extends dorsally to approximate the anterior opening of the pterotic sensory canal, lacking any contact with the laterosensory canal segment in the frontal. Given the generality of a tripartite laterosensory canal segment in the sixth infraorbital of proximate curimatid outgroups and among characiforms as a whole, the simple laterosensory system in the sixth infraorbital in *Steindachnerina, Pseudocurimata, Curimatella,* and *Cyphocharax* is hypothesized as derived (SYNAPOMORPHY 96).

OPERCULAR APPARATUS

Opercle and Subopercle

The close morphological and functional association of the opercle and subopercle makes it most efficient to discuss these elements jointly. The Curimatidae as a whole demonstrates a posteroventral truncation of the opercle and the associated expansion of the subopercle relative to the condition of these elements in examined outgroups. These modifications are, however, difficult to quantify non-arbitrarily, and thus I prefer not to utilize them as synapomorphies for the members of the Curimatidae, a clade that is already delimited by numerous uniquely derived characters. Within the Curimatidae, the opercle is significantly expanded posteriorly in all *Potamorhina* species relative to the condition in the outgroups. That expansion of the opercle in conjunction with the overall posterodorsal reorientation of the originally vertical primary axis of the opercle results in a pronounced inclination of the line of junction between the opercle and subopercle (see Vari, 1983, fig. 22). These modifications in the overall form and relative position of the opercle are together considered to be a synapomorphy for the species of *Potamorhina* (SYNAPOMORPHY 73).

Interopercle

The interopercle, the element lying ventral of the preopercle, and anterior of the subopercle and the anteroventral portion of the opercle is modified to some degree in all curimatids relative to the condition in the outgroups and also demonstrate a degree of variability within the family. In proximate outgroups to the Curimatidae the ossification is only vertically developed to a moderate extent in the region where it abuts the opercle and subopercle (see Winterbottom, 1980, fig. 33 for Anostomidae; Géry, 1964b, fig. 1 for Chilodontidae; and Vari, 1983, fig. 28 for Prochilodontidae). A somewhat more pronounced development posteriorly of the interopercle is typical for all curimatids. The intrafamilial variation in the form of the interopercle makes it difficult to non-arbitrarily define discrete characters within that continuum. Thus this feature is not used as a synapomorphy for the species of the family, which share numerous other synapomorphies.

The continuum between the forms of the interopercle within the Curimatidae also makes it difficult to non-arbitrarily discriminate character states for this element. As a consequence it is possible to only recognize readily a single derived condition of the interopercle within the family. In all *Potamorhina* species the interopercle is significantly further developed posteriorly into a triangular plate filling the space between the rear of the preopercle and the anterior margin of the opercle and subopercle (see Vari, 1983, fig. 22). This apomorphous expansion is considered a synapomorphy for *Potamorhina* (SYNAPOMORPHY 74).

LIGAMENTUM PRIMORDIALE

The A_1 section of the adductor mandibulae muscle in curimatids extends anteriorly from the preopercle to an attachment on the posterdorsal portion of the lower jaw. Arising from the anterodorsal portion of the adductor mandibulae and the proximate portions of the angulo-articular is a tendonous band that extends anterodorsally to an insertion either on the posterior margin (*Curimatopsis* species) or the medial surface of the main portion of the maxilla (all other curimatids). The ligament gradually tapers dorsally, without any marked shift in form or size. That band, the ligamentum primordiale (the primordial ligament of Winterbottom, 1974:232, and the articular-maxillary ligament of Alexander, 1964:183), arises in most characiforms from an aponeurotic sheet on the anterodorsal portion of A_1 and the proximate portions of the angulo-articular.

Although the area of origin of the ligament and the degree of its association with the angulo-articular varies within characiforms, the described morphology of the band is typical for all examined outgroups in the order. Within the Curimatidae such a relatively straight, cord-like ligamentum primordiale is found only in the species of *Curimatopsis*. All the remaining members of the family have the ligamentum primordiale complex modified to varying degrees. The species of *Potamorhina* and *Curimata* have the aponeurotic sheet on the anterodorsal portion of A_1 that typically serves as the origin of the ligamentum primordiale greatly expanded into a discrete thick connective tissue mass at the base of the main portion of the ligament. That thickening lies proximate to and is anteroventrally attached by connective tissue to the posterodorsal margin of the angulo-articular but structurally remains relatively distinct from the lower jaw.

This expanded ventral portion of the ligamentum primordiale complex in *Curimata* and *Potamorhina* is further modified in the genera *Psectrogaster, Steindachnerina, Pseudocurimata, Curimatella,* and *Cyphocharax.* Those taxa have a discrete dense mass centered along the longitudinal axis of the ligament. That body largely replaces the expanded fibrous connective tissue body found on the proximal section of the ligamentum primordiale in *Curimata* and *Psectrogaster.* Histological examination has shown that the body included in the ligamentum primordiale consists of cartilage enclosed within a aponeurotic sheet of varying thickness (Figure 37). The anterior portion of the cartilage serves as an area of attachment for a relatively extensive portion of the ligamentum primordiale. Posteriorly the cartilage body is continuous with the tendenous fibers of the anterior portion of the A_1 section of the adductor mandibulae muscle. The entire cartilage-ligament complex attaches via loose ligamentous bands to the posterodorsal margin of the angulo-articular. As is the case of the thickened connective tissue body in *Curimata* and *Potamorhina,* the ligamentum primordiale cartilage in *Psectrogaster, Steindachnerina, Pseudocurimata, Curimatella,* and

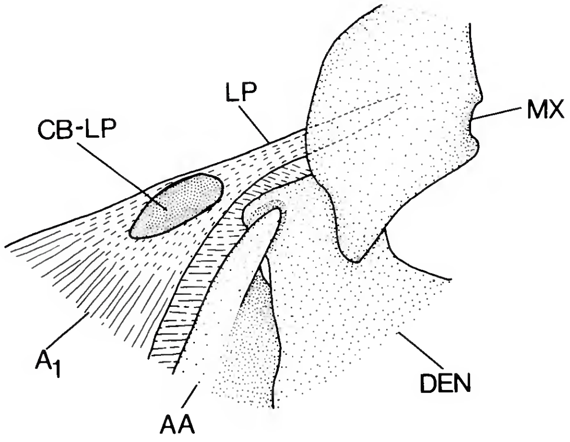

FIGURE 37.—Ligamentum primordiale, cartilage body of ligamentum primordiale, and proximate portions of A_1 section of adductor mandibulae muscle, maxilla, dentary, and angulo-articular of *Steindachnerina bimaculata*, USNM 261450. (Jaws in open position, continuation of ligamentum primordiale medial to maxilla indicated by dashed lines, right side, lateral view, anterior to right, dense patterned stippling represents cartilage.)

Cyphocharax is not directly associated with the lower jaw.

These modifications and elaborations of the proximal portions of the ligamentum primordiale are unique to the cited genera of the Curimatidae among examined characiforms and are considered to represent synapomorphies at two different levels of universality within the Curimatidae. The possession of some form of elaboration of the proximal portion of the ligamentum primordiale, either with or without an included cartilage body, is hypothesized to be a synapomorphy for the genera *Potamorhina, Curimata, Psectrogaster, Steindachnerina, Pseudocurimata, Curimatella,* and *Cyphocharax* (SYNAPOMORPHY 58). The presence of a cartilage mass in the ligamentum primordiale connective tissue complex is, in turn, hypothesized to be a further derived synapomorphy for the assemblage consisting of *Psectrogaster, Steindachnerina, Pseudocurimata, Curimatella,* and *Cyphocharax* (SYNAPOMORPHY 84).

UPPER AND LOWER JAWS

The most obvious distinguishing character of the curimatid jaws, upper and lower, is the absence of oral dentition in adults of the family. Juveniles of *Curimata cyprinoides* of up to approximately 25 mm SL have a single row of unicuspidate teeth in each jaw. Comparable dentition has been reported for *Steindachnerina elegans* by Azevedo et al. (1938, figs. 1, 2) and for several upper Rio Paraná curimatid species by de Godoy (1975:589, 596, 601). As juveniles of the Curimatidae alter their diet from zooplankton to detritus, this larval dentition is completely lost in all specimens above 30 mm SL. The vast majority of characiforms have some form of dentition, typically well developed, as adults and the absence of jaw teeth in adult curimatids is considered a synapomorphous reduction for the family (SYNAPOMORPHY 16).

The only other members of the Characiformes lacking jaw teeth as adults are *Anodus elongatus* Spix and *Eigenmannina melanopogon* (Cuvier) of the Hemiodontidae. As noted under "Synapomorphy List and Phylogenetic Reconstruction," this similarity is considered to represent a homoplasious loss of teeth in the hypothesized ancestoral species of the Curimatidae and in the lineage consisting of *Anodus* and *Eigenmannina* in the Hemiodontidae rather than a synapomorphy of Curimatidae and those taxa.

Premaxilla (PMX)

The premaxillae of curimatids are joined across the midline by connective tissue bands and attached to the ethmoid both through broad connective tissue sheets and via discrete ligaments. The range in the relative size and overall position of the mouth in different subunits of the family is reflected in the variety of premaxillary forms found among curimatids. Most of this variation, however, forms a continuum that is difficult, if not impossible, to non-arbitrarily subdivide into discrete units and thus it is not readily used in phylogenetic analyses. Two different discrete modifications of the premaxilla are recognizable, however, and serve to delimit assemblages of genera within the Curimatidae.

The premaxilla of the proximate outgroups to the Curimatidae, the families Prochilodontidae, Anostomidae and Chilodontidae, are all apomorphously modified in overall form (Vari, 1983:9) making them inappropriate as outgroups for evaluating the plesiomorphous form of the premaxilla among curimatids. As a consequence more distant outgroups, albeit of inexact phyletic position relative to the Curimatidae, were utilized. These examinations have shown that the generalized condition of the premaxilla in those characiform outgroups is a relatively well developed bone with a definite triangular form in dorsal or anterodorsal view. Such a premaxilla is characteristic of the vast majority of curimatids. The members of the genus *Curimatopsis*, alternatively, have an extremely elongate premaxilla that gradually tapers laterally to a curved rod-like shaft. The unique nature of this form of premaxilla within the Curimatidae and proximate outgroups results in its being considered a synapomorphy for the members of *Curimatopsis* (SYNAPOMORPHY 47).

The second alteration of the premaxilla that characterizes a subunit of the Curimatidae involves the mode of articulation between the premaxilla and maxilla. The posteroventral margin of the premaxilla extends a short distance lateral to the anterior margin of the main body of the maxilla. The point of contact between those elements in *Potamorhina, Psecterogaster, Steindachnerina, Pseudocurimata, Curimatella,* and *Cyphocharax* is elaborated into a discrete joint with an articular facet on both the premaxilla and maxilla at their point of contact. These modifications of the two bones at their area of articulation is considered to be a synapomorphy for the genera *Potamorhina, Curimata, Psectrogaster, Steindachnerina, Pseudocurimata, Curimatella,* and *Cyphocharax* given the absence of such structures in the examined characiform outgroups (SYNAPOMORPHY 59).

Maxilla (MX)

The maxilla, the second element of the upper jaw, demonstrates a number of discrete modifications within the Curimatidae, several of which are pertinent to the generic-level phylogeny in the family. Outgroup comparisons to determine the plesiomorphous condition of the maxilla within the Curimatidae are obscured by the apomorphous modifications of the maxilla in each of the proximate sister groups of the Curimatidae (Prochilodontidae, Anostomidae, and Chilodontidae). Outgroup comparisons to more distantly related characiform taxa of uncertain phylogenetic relationship relative to the clade formed by those three families and the Curimatidae nonetheless allow the advancement of a hypothesis of the generalized condition of the bone. Based on those comparisons, the generalized characiform condition of the maxilla is considered herein to be a moderately developed, laterally flattened blade-like body ventrally which is continuous dorsally with the dorsal rod-like articular process (e.g., various glandulocaudine species, Weitzman and Fink, 1985, figs. 59–66). Such a form of the maxilla is not encountered in the Curimatidae but a variety of derived overall morphologies of the bone do characterize subunits of the family.

Curimatopsis has a paddle-shaped, laterally flattened main body of the maxilla. The attachment of the ligamentum primordiale (LP) onto the maxilla is at the rear of the ossification in the area where the dorsal process of the maxilla joins the main body of the bone (AI, Figure 38A). Such an area of attachment is generalized for examined characiforms including the Anostomidae and Chilodontidae and is thus considered plesiomorphous. As a consequence of the highly modified form of the oral jaws in the Prochilodontidae, it is not possible to utilize the condition in that family for outgroup comparisons. The anteriorly expanded paddle-shaped main body of the bone characteristic of *Curimatopsis,* in contrast, is encountered in only a few characiform outgroups (e.g., *Thrissobrycon pectinifer* Böhlke, 1953, fig. 1). In light of its unusual nature within characiforms the condition of the maxilla in *Curimatopsis* is consequently considered a synapomorphy for the species of *Curimatopsis* (SYNAPOMORPHY 48).

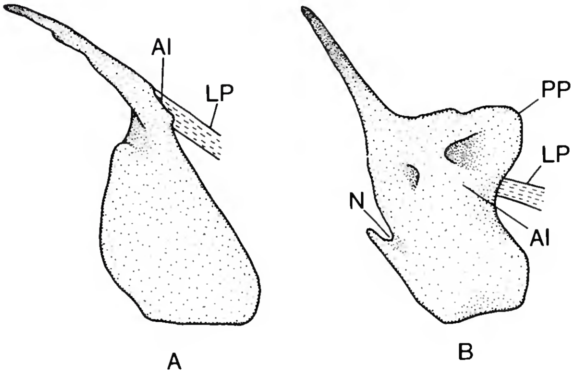

FIGURE 38.—Maxilla and anterodorsal portion of ligamentum primordiale: A, *Curimatopsis microlepis,* USNM 268867; and B, *Psectrogaster ciliata,* USNM 269990. (Left side, lateral view, anterior to left, area of insertion of ligamentum primordiale on maxilla not obvious in lateral view, point on lateral surface overlying insertion indicated by "AI".)

The species of *Potamorhina, Curimata, Psectrogaster, Steindachnerina, Pseudocurimata, Curimatella,* and *Cyphocharax* have a dramatically different morphology of the maxilla. In all the species of those genera the anterior margin of the bone is only slightly developed, often with a notch to accommodate the lateral portion of the premaxilla (N, Figure 38B). The posterodorsal portion of the main body of the maxilla, alternatively, is developed into a large plate-like process (PP) that extends under the first infraorbital when the mouth is closed. The attachment of the ligamentum primordiale in these taxa (AI) is now on the medial surface of the maxilla at the anterior margin of this expanded posterodorsal process. Utilizing that point of attachment as a homologous landmark, it appears that the posterodorsal process of the maxilla is the consequence of an expansion of that region of the bone. Given the absence of such a process on the maxilla in other examined characiforms, the possession of that structure is considered derived and a synapomorphy for the genera *Potamorhina, Curimata, Psectrogaster, Steindachnerina, Pseudocurimata, Curimatella,* and *Cyphocharax* (SYNAPOMORPHY 60). As noted above, these taxa also have in common the derived possession of an articular facet on the dorsal margin of the maxilla which contacts a comparable process on the premaxilla.

Dentary (DEN)

The dorsal margin of the dentary bone typically is anteriorly straight or slightly convex, and posteriorly distinctly convex in the proximate outgroups to the Curimatidae, the families Prochilodontidae, Anostomidae and Chilodontidae (see Vari, 1983, fig. 2). That condition, hypothesized as plesiomorphous for the Curimatidae, is also found in the family in all members of *Curimatopsis* (Figure 39A). The remainder of the family Curimatidae, in contrast, has a sigmoid dorsal margin to the dentary, with the convex central portion of the bone flanked by two concave regions (Figure 39B). The centrally convex region, hypothesized as derived relative to the condition in *Curimatopsis* and the outgroups to the Curimatidae, is thus

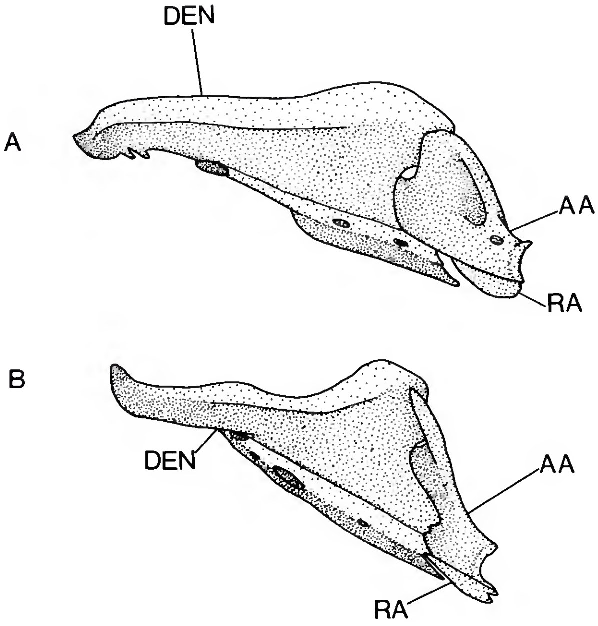

FIGURE 39.—Lower jaw: A, *Curimatopsis microlepis*, USNM 268867; and B, *Curimatella alburna*, MZUSP 6309. (Left side, lateral view, anterior to left.)

considered a synapomorphy for *Potamorhina, Curimata, Psectrogaster, Steindachnerina, Pseudocurimata, Curimatella,* and *Cyphocharax* (SYNAPOMORPHY 61). It demonstrates notable variation within the family. In some taxa (e.g., *Curimata*) it is developed into a distinct, somewhat triangular process, whereas in others (e.g., *Potamorhina*) it curves laterally into a bony lip. The non-*Curimatopsis* curimatids cannot feasibly be non-arbitrarily divided into discrete subsets based on this variation. I consequently will not utilize those differences at less inclusive phylogenetic levels.

PALATINE ARCH

The palatine arch consists of four bones, the palatine, ectopterygoid, mesopterygoid, and metapterygoid, and their associated cartilages. In the majority of characiforms those elements form a closely interconnected complex extending between the upper jaw, ethmo-palatine cartilage and vomer anterodorsally, the quadrate ventrally and the hyomandibula posteriorly. Each of the components of the palatine arch demonstrates derived modifications pertinent to the question of the monophyly of the Curimatidae and various subunits of that family. In order to simplify the discussion and evaluation of the polarities of each of these alterations, the morphology of each component of the arch will be discussed individually.

Palatine (PAL) and Ethmo-palatine Cartilage (EPC)

One character of the palatine synapomorphous for all the species of the Curimatidae was previously discussed in detail by Vari (1983:26). The most common condition of the palatine in characiform outgroups has a single anterodorsal cartilaginous articular surface contacting the vomerine region of the neurocranium and the ethmo-palatine cartilage associated with the upper arm of the premaxilla (the submaxillary cartilage of Daget, 1964, fig. 23). All species of the Curimatidae differ from that hypothesized plesiomorphous arrangement in having an additional, distinct cartilage-capped process on the posterodorsal surface of the bone (PDAS, Figure 40A,B). That cartilage articulates with a corresponding process on the anteroventral surface of the ventral wing of the lateral ethmoid (Vari, 1983, fig. 25). Although a second articular surface on the palatine somewhat comparable to that in the Curimatidae is approximated to varying degrees in some characiform outgroups, both in the Neotropical and Ethiopian realms, such a structure is absent in the proximate outgroups to the Curimatidae, the families Prochilodontidae, Anostomidae, and Chilodontidae. The absence of a cartilage capped-articular surface contacting the lateral ethmoid in those taxa in conjunction with the morphological differences in the form of similar processes in those characiform outgroups with such modifications is congruent with the hypothesis that the posterodorsal articular process of the palatine characteristic of the Curimatidae (SYNAPOMORPHY 21) is derived for that family (see Vari, 1983:26, for a more detailed discussion).

Within the Curimatidae, the palatine shows a second set of modifications that are common to *Potamorhina, Curimata, Psectrogaster, Steindachnerina, Pseudocurimata, Curimatella,* and *Cyphocharax.* All species of *Curimatopsis* (Figure 40A) have a continuous elaborate cartilage that extends along the anterior face of the palatine (PAL), continues along the dorsomedial margin of the bone, and expands posterodorsally into the distinct secondary articular process (PDAS) described above. The cartilage then continues posteroventrally along the lateral surface of the palatine arch in the region of contact of the metapterygoid and ectopterygoid. In *Potamorhina, Psectrogaster, Curimata, Steindachnerina, Pseudocurimata, Curimatella,* and *Cyphocharax* the continuous palatine cartilage characteristic of *Curimatopsis* is subdivided into two discrete portions separated by a well ossified posteromedial region of the palatine (Figure 40B). Anteriorly and laterally the anterior cartilage articulates with the ethmo-palatine cartilage (EPC) and the vomer respectively. That cartilage is also characterized by a distinct central depression (Figure 40B) that is not present in *Curimatopsis.* The posterodorsal palatine articular cartilage (PDAS) is a discrete mass enveloped anteriorly, medially, and to varying degrees laterally by the ossified surface layer of the palatine. Ventrolaterally the posterolateral articular surface retains its continuity with the cartilaginous band overlying the junction between the metapterygoid and the ectopterygoid

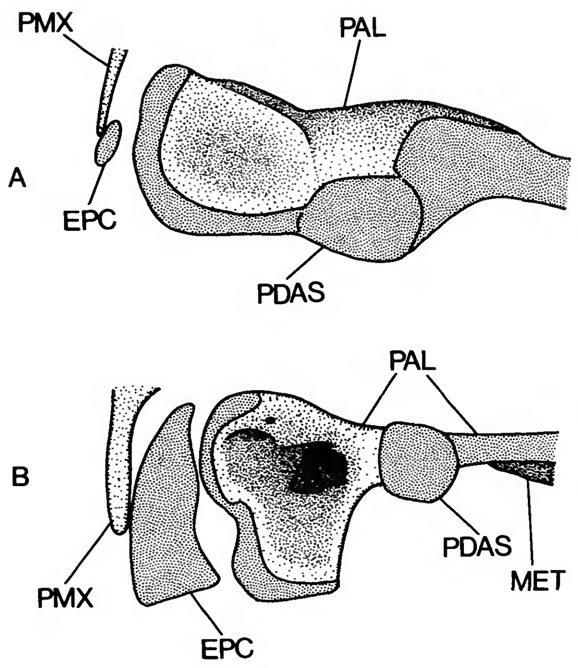

FIGURE 40.—Palatine, ethmo-palatine cartilage and proximate portions of premaxilla and metapterygoid: A, *Curimatopsis microlepis*, USNM 268867; and B, *Steindachnerina argentea*, USNM 285663. (Right side, dorsal view, anterior to left, dense patterned stippling represents cartilage.)

(Figure 40B). This subdivision of the palatine cartilage into two articular surfaces and the associated complex restructuring of the ossified portions of that element are unique to this assemblage of genera among examined characiforms and considered a synapomorphy for *Potamorhina, Curimata, Psectrogaster, Steindachnerina, Pseudocurimata, Curimatella,* and *Cyphocharax* (SYNAPOMORPHY 62).

The ethmo-palatine cartilage (EPC) is a distinct body situated between the posterior surface of the upper arm of the premaxilla and the anterior margin of the palatine. There is usually only a single cartilage mass lying between these bones, although that cartilage is apparently subdivided into two units in some taxa (e.g., the Old World characiform family Citharinidae, Vari, 1979:294). The ethmo-palatine cartilage is usually a relatively well developed thick body extending along most of the anterior margin of the palatine and much of the rear of the dorsal process of the premaxilla (e.g., *Steindachnerina argentea,* Figure 40B) to which it is relatively closely joined by connective tissue bands. Such a condition is found in the genera *Potamorhina, Psectrogaster, Curimata, Steindachnerina, Pseudocurimata, Curimatella,* and *Cyphocharax.* In the species of *Curimatopsis,* in contrast, the ethmo-palatine cartilage is reduced to a very small ovoid body along the posteromedial surface of tip of the premaxilla (Figure 40A). That condition represents a significant reduction in the relative size of the cartilage that is considered a synapomorphy for the members of the genus (SYNAPOMORPHY 49).

Ectopterygoid (ECT)

The ectopterygoid shows a wide range in overall morphology within the Curimatidae, although most of the variation cannot be non-arbitrarily apportioned into discrete characters. One distinct difference, distinguishing *Curimatopsis* from the remainder of the family, involves the form of the anterior margin of the ectopterygoid. That region of the bone is unelaborated and transversely rounded in the species of *Curimatopsis* but has a distinct flattened vertical flange in *Potamorhina, Curimata, Psectrogaster, Steindachnerina, Pseudocurimata, Curimatella,* and *Cyphocharax.* The condition of the elements in *Curimatopsis* is similar to that in most characiforms, and within the context of such an outgroup analysis would be evaluated as being plesiomorphous. The Prochilodontidae, the sister group to the Curimatidae, however, has a highly modified ectopterygoid that is distinctly flattened transversely. It is thus possible that the flange along the anterior margin of the bone in non-*Curimatopsis* curimatids is at least in part homologous with the anterior portion of the flattened prochilodontid ectopterygoid. If that is the case, then the *Curimatopsis* form of the ossifications would be a derived secondary reversal to the more generalized condition. Both hypotheses, that the *Curimatopsis* form of the ectopterygoid is derived, or that it is plesiomorphous, would be congruent with the proposed overall most parsimonious phylogeny. Thus it is not possible to polarize the character by either outgroup comparisons or by reference to the overall most parsimonious hypothesis of intrafamilial relationships.

Mesopterygoid (MES)

The mesopterygoid is typically a relatively simple ossification situated between the palatine and metapterygoid, and lying dorsal of the quadrate (Figure 41A). The relative size of the element varies in different groups of characiforms, with the condition in the proximate outgroups to the Curimatidae being a small to moderate sized bone that is unelaborated along its dorsal margin. The mesopterygoid and metapterygoid which lie posterior to it along the palatine arch, are suspended from the neurocranium by a broad thin connective tissue sheet that attaches along the length of the dorsal margins of those ossifications.

The described suspensory system joining the mesopterygoid to the cranium is modified in all curimatids. Members of that family rather than retaining a broad connective tissue band between those regions, have instead a discrete ligamentous band that extends between the dorsal margin of the mesopterygoid and the ventral surface of the vomer. Within the

Curimatidae, this ligamentous band has two different shapes and forms of attachment to the mesopterygoid. In *Curimatopsis,* the ligamentous band is quite narrow dorsally, but progressively fans out ventrally to attach over a relatively broad region of the dorsal margin of the mesopterygoid. In *Potamorhina, Curimata, Psectrogaster, Steindachnerina, Pseudocurimata, Curimatella,* and *Cyphocharax* the ligament arises in a similar fashion from the vomer, but does not fan out ventrally, being rather more strap-like and of continuous width from the vomer to the mesopterygoid and attaching onto the latter element on a distinct dorsal process (AI, Figure 41A,B).

Thickenings within the broad connective tissue sheet between the palatine arch and neurocranium standard for most characiforms are found in various taxa, including the genus *Ichthyoelephas* in the Prochilodontidae. Those ligamentous bands, however, are not as discrete as those within the Curimatidae, nor do they have the same areas of attachment. Thus those structures are considered non-homologous with the discrete ligament between the vomer and mesopterygoid characteristic of the Curimatidae. Given the broad area of attachment of the connective tissue sheet typically joining the palatine arch and the neurocranium in characiforms, these reductions in the area of attachment of the connective tissues extending between the vomer and mesopterygoid in curimatids are treated as derived.

In the Curimatidae, such reductions in the area of attachment are considered apomorphous at two levels of universality. The possession of a fan-shaped or strap-like thickened connective tissue band arising from a restricted area on the vomer and having either a broad or narrow attachment on the mesopterygoid is hypothesized a synapomorphy for all members of the Curimatidae (SYNAPOMORPHY 34). The presence of a strap-like ligament of constant width with a discrete further restricted area of attachment to the mesopterygoid, in comparison with the more extensive area of attachment in *Curimatopsis* and characiform outgroups, is, in turn, hypothesized to be a shared derived character for *Potamorhina, Curimata, Psectrogaster, Steindachnerina, Pseudocurimata, Curimatella,* and *Cyphocharax* (SYNAPOMORPHY 63).

The mesopterygoid in characiforms most commonly lies dorsal of the junction of the posterodorsal portion of the quadrate and the anteroventral region of the metapterygoid, with those elements meeting along a synchondral joint below the mesopterygoid. A majority of characiforms have a moderately to well developed aperture, the metapterygoid-quadrate fenestra (MQF, Figure 41A), delimited anteriorly and ventrally by the quadrate (QU), dorsally and posteriorly by the metapterygoid (MET) and sometimes posteroventrally by the symplectic (SYM) (e.g., *Brycon meeki,* Weitzman, 1964, fig. 10). Such an association of bones and cartilages is considered plesiomorphous in light of comparisons to both proximate outgroups to the Curimatidae and diverse other characiforms. Within the Curimatidae that pattern of bones also occurs in the species of *Curimatopsis* and *Potamorhina* (Figure 41A). The species of *Psectrogaster, Steindachnerina, Pseudocurimata, Curimatella,* and *Cyphocharax* have the mesopterygoid significantly modified. In those genera, the mesopterygoid no longer terminates ventrally distinctly short of the dorsal margin of the metapterygoid-quadrate fenestra. Rather the mesopterygoid is further expanded ventrally over the medial surface of the junction of the metapterygoid and quadrate and continues partially or completely across the anterior portion of the metapterygoid-quadrate fenestra (Figure 41B). This extension of the mesopyterygoid results in the subdivision of that fenestra to varying degrees into anterior (ASMQF) and posterior (PSMQF) sections. Such an elaboration of the mesopterygoid, and the assocated subdivision of the metapterygoid-quadrate fenestra has not been encountered in any examined characiform outgroups. That ventral expansion of the mesopterygoid is consequently considered a synapomorphy for the clade consisting of *Psectrogaster, Steindachnerina, Pseudocurimata, Curimatella,* and *Cyphocharax* (SYNAPOMORPHY 85).

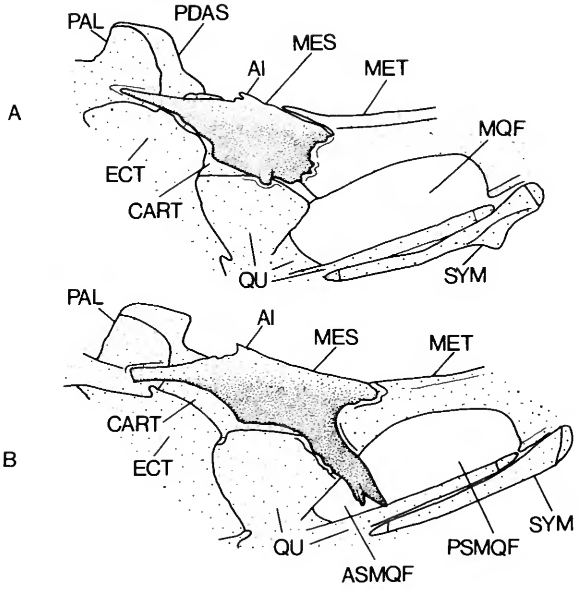

FIGURE 41.—Mesopterygoid: A, *Potamorhina laticeps,* USNM 121325; and B, *Psectrogaster ciliata,* USNM 26990. (Right side, medial view, anterior to left, proximate portions of neighboring bones outlined and lightly stippled.)

Metapterygoid (MET)

Vari (1983:28) noted that members of the Curimatidae have an apomorphous elaboration of the metapterygoid consisting of a ridge extending along the medial surface of the bone for at least part of its length. That condition, hypothesized to be a synapomorphy for the members of the Curimatidae (SYNAPOMORPHY 23), is further developed in various sublineages of the family. The ridge (METR) is only moderately developed in *Curimatopsis* (Figure 42A) and *Potamorhina* (Figure 42B), but is much more pronounced in *Curimata* (Figure 42D), *Psectrogaster* (Figure 42C), *Steindachnerina, Pseudocurimata, Curimatella,* and *Cyphocharax* in which it extends across the entire length of the bone. This more extensive development of the metapterygoid ridge is hypothesized to be a more derived condition in light of the absence of any form of the ridge in examined outgroups and relative to the less developed ridge in *Curimatopsis* and *Potamorhina.* The possession of such a process is thus considered a synapomorphy for *Curimata, Psectrogaster, Steindachnerina, Pseudocurimata, Curimatella,* and *Cyphocharax* (SYNAPOMORPHY 77).

The species of *Curimata* have the ridge on the medial surface of the metapterygoid considerably thickened anteriorly (Figure 42D). This expanded region of the bone is continuous anteriorly with the comparably expanded region on the posteromedial portion of the mesopterygoid that serves as the area of attachment for the ligament extending between that element and the vomer. This expansion of the anterior portion of the metapterygoid, unique to the species of *Curimata,* is hypothesized synapomorphous for the genus (SYNAPOMORPHY 83).

As noted in the discussion of the mesopterygoid in the previous section, the metapterygoid and quadrate jointly delimit a usually relatively large, rotund, or horizontally oblong aperture in the middle portion of the suspensorium. That opening, the metapterygoid-quadrate fenestra, is widely distributed within the Characiformes, being found in the Neotropical Characidae (*Brycon,* Weitzman, 1962:46, fig. 10; *Acestrorhynchus* Eigenmann and Kennedy, Roberts, 1969, fig. 32), Ctenoluciidae (*Ctenolucius* Gill, Roberts, 1969, fig. 28), Erythrinidae (*Hoplias,* Roberts, 1969, fig. 29), Hemiodontidae (*Hemiodus,* Roberts, 1974, fig. 7), Parodontidae, Prochilodontidae (*Ichthyoelephas,* Vari, 1983, fig. 28), and Anostomidae (Winterbottom, 1980, fig. 35), and in the Old World families Characidae (*Alestes, Hydrocynus* [Brewster, 1986, fig. 8], and *Phenacogrammus*), Hepsetidae (*Hepsetus* Swainson), Citharinidae (*Citharinus,* Daget, 1962a, fig. 9; *Citharidium,* Daget, 1962b, fig. 13), and most members of the Distichodontidae (*Xenocharax,* Daget, 1960, fig. 10). Although this fenestra is subdivided by a posteroventral process of the mesopterygoid in most genera of the Curimatidae (see previous section), the overall form of opening characteristic of most characiforms is found in all curimatids other than the species of *Curimatopsis.* In that genus the fenestra is nearly erradicated by the ventral expansion of the metapterygoid which extends nearly to the

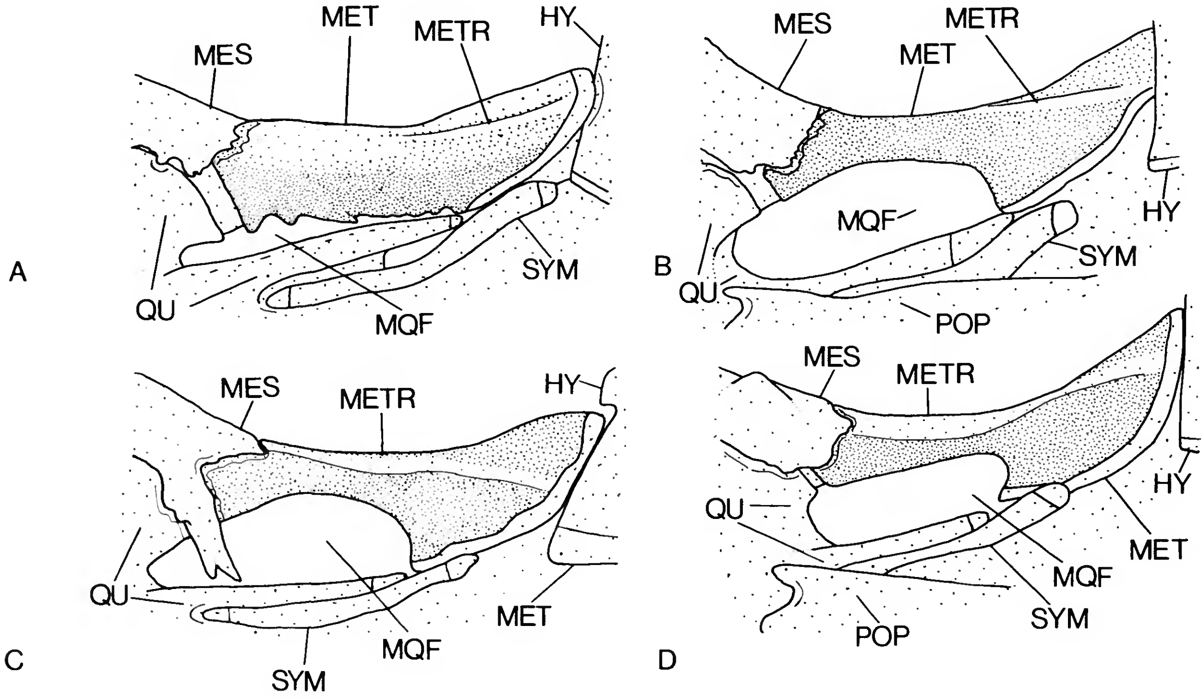

FIGURE 42.—Metapterygoid: A, *Curimatopsis microlepis,* USNM 268867; B, *Potamorhina altamazonica,* USNM 257367; C, *Psectrogaster ciliata,* USNM 269990; and D) *Curimata cyprinoides,* USNM 267964. (Right side, medial view, anterior to left, proximate portions of neighboring bones outlined and lightly stippled.)

dorsal margin of the posterior portion of the quadrate (Figure 42A). This reduction in the extent of the aperture differs from the diminished opening in some members of the Old World characiform family Distichodontidae in the mode in which it is achieved. In the distichodontid *Neolebias spilotaenia* Boulenger the reduced fenestra is a consequence of the expanded symplectic rather than an enlarged metapterygoid (Vari, 1979:293). *Nannocharax* Günther and *Hemigrammocharax* Pellegrin of the same family (see Daget, 1961, fig. 10), along with members of the Neotropical family Lebiasinidae (see Weitzman, 1964, fig. 7) have the quadrate approximating the metatpterygoid as a consequence of the reduced vertical extent of the entire suspensorium rather than due to an expansion of individual elements. The conditions in those outgroup families thus all differ from that found in *Curimatopsis*.

A near or total elimination of the fenestra by an expanded metapterygoid is found, however, in all members of the Chilodontidae. The closest relatives to the Chilodontidae, the family Anostomidae is, in contrast, characterized by the presence of a fenestra (see Winterbottom, 1980, fig. 35). Similarly the Prochilodontidae, the sister group to the Curimatidae, has a complete metapterygoid-quadrate fenestra typical of characiform outgroups (e.g., *Ichthyoelephas*, Vari, 1983, fig. 28) as do all curimatids other than *Curimatopsis*. It is thus most parsimonious to assume that the conditions in the Chilodontidae and *Curimatopsis* are homoplasious. The *Curimatopsis* condition of a reduction of the metapterygoid-quadrate fenestra as a consequence of the expansion of the metapterygoid is thus considered a synapomorphy for the members of the genus (SYNAPOMORPHY 39).

SUPRANEURALS (SN_{1-6})

A series of midsagittal ossifications are typically found dorsal of the vertebral column in the region between the rear of the neurocranium and the anteriormost proximal radial pterygiophore of the dorsal fin. These bones, the supraneurals, along with the proximal radial pterygiophores of the dorsal fin interdigitate basally between the distal portions of the neural spines of the proximate vertebrae. In the following discussion and in Figure 43 neural spines are numbered sequentially from the spine of the first free vertebrae posterior of the Weberian complex.

The typical pattern for these elements in the Curimatidae is that shown in Figure 43A. Two supraneurals are located anterior of the first neural spines (the two anterior supraneurals are sometimes fused), with the third to fifth supraneurals and the second to fourth neural spines interdigitating sequentially. The basal portion of the first proximal radial pterygiophore of the dorsal fin interdigitates between the distal portions of the fourth and fifth neural spines. This pattern of supraneurals, neural spines, and the first proximal pterygiophore is generalized for the vast majority of curimatid species with three exceptions. Two nominal species in *Curimata* (*vittata* and *murieli*) have the number of supraneurals reduced to four. This reduction is apparently a consequence of the loss of the posterior supraneural, and as a consequence the most posterior element of that series in these species is located between the second and third neural spines. Associated with that reduction in the number of supraneurals is the shift anteriorly of the region of interdigitation of the basal portion of the first proximal pterygiophore of the dorsal fin to between the third and fourth neural spines, rather than between the fifth and sixth spines.

The species of *Pseudocurimata* have the opposite modification of the pattern of association of the supraneurals and the anterior proximal radial pterygiophore with the anterior neural spines. In that genus the anterior proximal pterygiophore of the dorsal fin inserts between the distal portions of the fifth and sixth, or sixth and seventh neural spines rather than between the fourth and fifth neural spines as in the vast majority of curimatids. Associated with that more posterior insertion of the fin is the absence of a supraneural or proximal pterygiophore either between the fourth and fifth, or fifth and sixth neural spines (Figure 43B,C).

Outgroup information on the polarity of the different

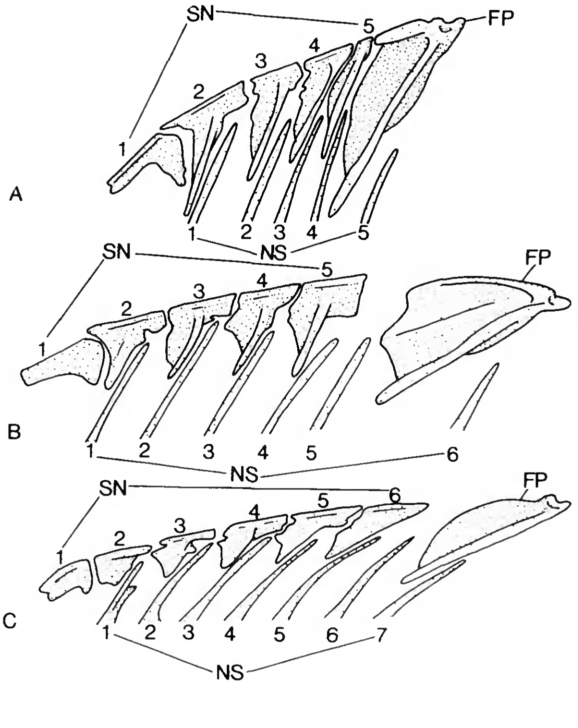

FIGURE 43.—Supraneurals, neural spines of proximate vertebrae, and first proximal radial pterygiophore of dorsal fin: A, *Curimata cyprinoides*, USNM 225619; B, *Psuedocurimata lineopunctata*, MCZ 54029; and C, *Pseudocurimata peruana*, USNM 285667. (Left side, lateral view, anterior to left.)

patterns of interdigitation is equivocal. Various species in the Prochilodontidae have the first proximal pterygiophore of the dorsal fin inserting either between the fourth and fifth or fifth and sixth neural spines, and demonstrate overall patterns of supraneurals, neural spines, and proximal pterygiophores comparable to those shown in Figure 43A,B. Members of the Anostomidae also show some variation in the interdigitation pattern of these elements, whereas the species of the Chilodontidae have the first proximal pterygiophore inserting between the fourth and fifth neural spines, with the overall pattern of that element, the neural spines, and supraneurals similar to the pattern of Figure 43A. Given the distribution of the various states within the Curimatidae and in its sister groups of varying degrees of proximity, it is most parsimonious to hypothesize that the position of the first proximal pterygiophore of the dorsal fin posterior of the fifth or sixth neural spines in *Pseudocurimata* is derived (SYNAPOMORPHY 102).

Such a posterior portion of the dorsal fin and the resultant gap in the sequence of interdigitations of elements between the neural spines immediately anterior to the first proximal pterygiophore of the dorsal fin that is general to all *Pseudocurimata* species also occurs in two other nominal species within the Curimatidae. *Curimata ocellata* and *C. semitaeniata*, elongate fusiform species of the Amazon basin have a pattern of supraneurals and the anterior proximal pterygiophore of the dorsal fin comparable to that of some *Pseudocurimata* species (e.g., *Pseudocurimata lineopunctata*, Figure 43B). The common occurrence of this derived pattern in *Curimata ocellata* and *C. semitaeniata* on the one hand, and *Pseudocurimata* species on the other is considered homoplasious within the context of the overall most parsimonious hypothesis of relationships.

CAUDAL FIN COMPLEX

The hypural complex and the rays of the caudal fin demonstrate a number of apomorphous modifications in *Curimatopsis* which were previously discussed and illustrated by Vari (1982a:5–9). Four of those characters involve sexually dimorphic features in which the derived condition is found only in the males. These apomorphies are the expansion of the posterior neural and haemal spines on the posterior two free centra into broad midsaggital plates (see Vari, 1982a, figs. 2, 4; SYNAPOMORPHY 35), the possession of basal spurs on the middle caudal-fin rays (see Vari, 1982a, fig. 5; SYNAPOMORPHY 36), the vertical expansion of the penultimate ray of the lower lobe of the caudal fin (see Vari, 1982a, fig. 5; SYNAPOMORPHY 37), and the close association of the ventralmost ray of the upper lobe of the caudal fin with the dorsalmost ray of the ventral lobe of that fin rather than the retention of the gap between those elements typical for characiforms (SYNAPOMORPHY 38). Further data on those characters and the conditions in those systems in outgroup taxa are found in Vari (1982a:5–9). Three other derived features of the caudal skeleton in *Curimatopsis*, the pronounced expansion of the penultimate principal caudal-fin ray of males (*Curimatopsis* SYNAPOMORPHY C), the possession of a second hypural free from $PU_1 + U_1$ but fused to the first hypural (*Curimatopsis* SYNAPOMORPHY D), and the contact in males of the third hypural with the fused first and second hypurals and the associated development posteriorly of interdigitations between those elements (*Curimatopsis* SYNAPOMORPHY E), were advanced as synapomorphies of the clade consisting of *C. crypticus* and *C. evelynae*. *Curimatopsis myersi* described subsequently (Vari, 1982b) has been found to also share these apomorphous features, and the more inclusive outgroup examinations associated with this study has confirmed the derived nature of the characters.

An additional synapomorphy in the caudal skeleton pertinent to hypotheses of subgeneric relationships in *Curimatopsis* has also been uncovered in this study. In males of *C. evelynae*, *C. crypticus*, and *C. myersi*, the posterior two free preural centra and the fused $PU_1 + U_1$ have distinct longitudinal dorsoventrally flattened lateral flanges arising from their midlateral surface. The processes evidently extend into the connective tissue layer between the epaxial and hypaxial musculature, and serve an an area of attachment for various ligamentous bands. Such processes on those posterior vertebrae are unknown elsewhere in the Curimatidae, nor have they been encountered in the examined outgroups. The lateral flanges on these posterior vertebral elements are thus hypothesized to be synapomorphies for *Curimatopsis evelynae*, *C. crypticus*, and *C. meyersi* (*Curimatopsis* SYNAPOMORPHY G).

A reduction to one set of uroneurals from the two sets typical for characiforms was hypothesized to be a synapomorphy for the species of *Curimatopsis* (Vari, 1982a:4, 5; SYNAPOMORPHY 40), a polarity congruent with the findings of this project. Further analysis has shown that a greatly reduced or absent set of second uroneurals is also characteristic of all species of *Pseudocurimata*. Within an examined series of six cleared and stained individuals of *P. boulengeri*, three were found to lack any indication of a second set of uroneurals and in the other three specimens there were present only very small bones on each side of the hypural complex in the region typically occupied by the second uroneurals. No indication was found of the second set of uroneurals in the examined cleared and stained specimens of *P. peruanus* or *P. troscheli*, and only a greatly reduced set of second uroneurals was found in the examined cleared individuals of *P. lineopunctatus* and *P. patiae*. This pronounced reduction or complete loss of the second set of uroneurals is hypothesized synapomorphous for the members of *Pseudocurimata* (SYNAPOMORPHY 103). That character is considered to be homoplasiously present in *Curimatopsis* within the context of the overall most parsimonious hypothesis of relationships within the Curimatidae.

LATEROSENSORY SYSTEM OF BODY

The vast majority of characiforms have a completely developed laterosensory canal system on the body with all lateral line scales having minimally a pore opening to the surface, and with some species and groups having more elaborate canal systems within the scales. A completely pored lateral line occurs in all members of the proximate outgroups to the Curimatidae, the families Prochilodontidae, Anostomidae, and Chilodontidae. Within the Curimatidae a completely pored laterosensory system on the body characterizes all members of the Curimatidae with the exception of the species of *Curimatopsis* and a subset of *Cyphocharax* species (*saladensis, vanderi, punctata*). *Curimatopsis maulatus*, described by Ahl (1934) as having an incompletely pored laterosensory canal system, is actually a juvenile of a *Cyphocharax* species in which that system is fully developed in the adults (pers. observ.). Although the reduction in this poring is hypothesized as derived given the fully developed laterosensory canal systems of the outgroups, the distribution of that character is not congruent with the final phylogeny of this study (Figure 44). The character is thus considered homoplasious at the generic level, with the reduced development of poring of the lateral line hypothesized synapomorphous for *Curimatopsis* species on the one hand (SYNAPOMORPHY 50) and the cited *Cyphocharax* species on the other.

A possible correlation exists between the reduced degree of poring of the laterosensory canal system of the body and the relatively small body size of many of the species with that character. Although paedomorphic features including a reduction in the degree of the development of the laterosensory canal system are often associated with relative miniaturization (Weitzman and Vari, 1988), the concept of such a direct correlation would appear at first to be qualified when applied to the Curimatidae since *Curimatopsis microlepis*, a species which achieves at least 90 mm SL, has an incompletely pored lateral-line. The concept of a miniature and the correlated suggestion of paedomorphosis is, nonetheless, applicable even to *C. microlepis* given the much larger body sizes of all members of the Prochilodontidae, the sister group to the Curimatidae, and proximate sister groups to *Curimatopsis* within the Curimatidae (see also discussion under "Convergent Characters").

SQUAMATION

The species of the Curimatidae are characterized by complete squamation of the body, but without basal sheaths of scales on the dorsal or anal fin such as occur on the anal fin in the characid *Markiana* Eigenmann. Similarly the squamation on the caudal fin terminates only slighty posterior of the base of the caudal fin rays in the vast majority of the members of the Curimatidae. The one exception involves the species of *Curimatella*. Although juveniles of the genus have only a limited degree of squamation at the base of the caudal fin comparable to the situation in curimatid outgroups, there is an ontogenetic increase in the extent of squamation, with adults having scales over much of the proximate two-thirds of both lobes of the caudal fin.

The absence of such an extensive patch of scales on the caudal fin lobes, the condition in the remainder of the Curimatidae, is also characteristic of the Prochilodontidae and Chilodontidae, along with all genera of the Anostomidae other than for the few species of the genus *Leporellus* Lütken. Within the context of the overall phylogenetic hypothesis for the clade consisting of the Curimatidae, Prochilodontidae, Anostomidae, and Chilodontidae (Vari, 1983), the presence of caudal fin squamation in *Curimatella* is most simply considered synapomorphous for the members of the genus (SYNAPOMORPHY 104), albeit independently derived within the Anostomidae.

The relative size of body scales within the family Curimatidae as reflected in the number of scales along the lateral line from the supracleithrum to the base of the caudal fin demonstrates a nearly four fold range. That variation forms, however, a near continuum that makes it impossible to non-arbitrarily utilize much of that data for phylogenetic studies. Two exceptions involve the very high lateral-line counts for the species of *Potamorhina*, along with *Cyphocharax abramoides*. Vari (1984a:7) noted that the species of *Potamorhina* have 85–110 scales in that series, overlapping within the Curimatidae only with *Cyphocharax abramoides* (77–95 lateral line scales). The remainder of the family have 26 to 76 pored scales in a longitudinal series, and the Prochilodontidae, the sister group to the Curimatidae, typically has less that 80 lateral-line scales (R.M.C. Castro, pers. comm.). Thus the condition in *Potamorhina* is judged to be synapomorphous for the species of the genus (SYNAPOMORPHY 69) (see Vari, 1984a:7 for more details). The increased, although not as numerous, lateral line scales of *Cyphocharax abramoides* are considered to represent a homoplasious increase in that series.

Synapomorphy List and Phylogenetic Reconstruction

The previous section of the discussion details the numerous derived modifications of and within the Curimatidae over a variety of body systems that were discovered in the course of this and previous studies (Vari, 1982a, 1983, 1984a). Vari (1983:48) hypothesized that the Curimatidae and Prochilodontidae were sister groups, and that the Curimatidae (not including *Anodus* Spix and *Eigenmannina* Fowler) was a monophyletic assemblage. The anatomical studies associated with this project have uncovered additional information congruent with both of those hypotheses. The data from the examined body systems is also both relevant to a hypothesis of generic level relationships within that family, and to the evaluation of previously proposed genera.

In the following, shared derived characters congruent with a hypothesis of monophyly of the group consisting of the Prochilodontidae and Curimatidae will be discussed first. The majority of the characters supporting the hypothesis of the monophyly of that bifamilial lineage were analyzed and listed by Vari (1983) and all are noted again below. Some of these were not redescribed in detail in the preceeding sections of this paper, and the reader is referred to Vari (1983) for detailed information on those characters. Additional synapomorphies for the Curimatidae and Prochilodontidae were discussed in preceeding character descriptions, and are also listed below. The enumeration of the synapomorphies for the clade formed by those two families is followed by a listing and discussion of the less universal apomorphous states that characterize the Curimatidae, and the clades, named and unnamed, within that family.

A variety of alternative schemes have been proposed to convey phylogenetic information within a classification. A number of these systems involve the proposal of a name for each clade defined by shared derived characters, a method that would necessitate a number of taxa between the generic and familial levels in the Curimatidae. Formal nomenclatural recognition is given in this study only to the family and the major terminal sublineages recognized as genera. This simplified nomenclatural system is used since the recognition of taxa between the generic and familial levels for those subfamilial clades consisting of two or more genera would necessitate the proposal and utilization of at least four suprageneric taxa, a number that would increase if the terminal polychotomy were to be resolved by future studies. The resultant proliferation of suprageneric taxa within the family would do little to clarify the following discussion, or indeed might obfuscate the presentation. Although the proposed scheme of relationships cannot as a consequence be directly

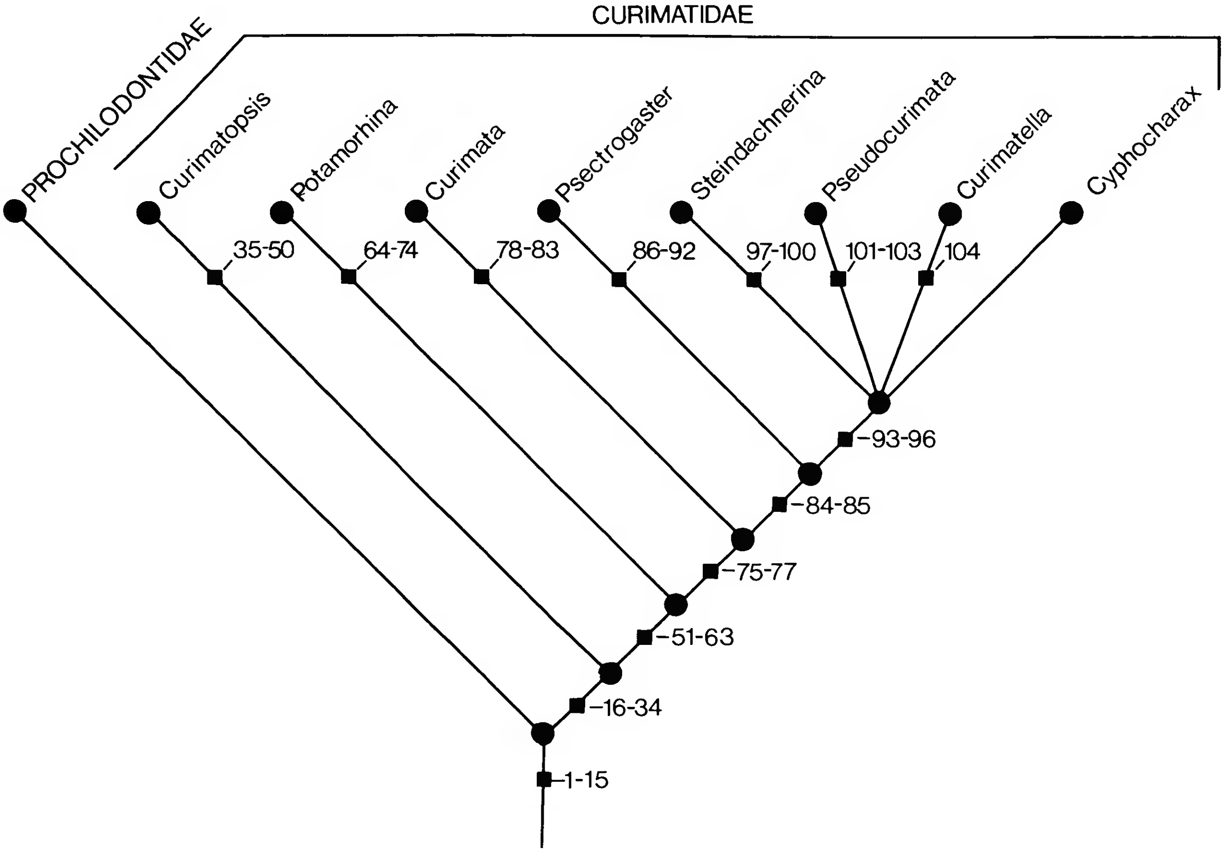

FIGURE 44.—Cladogram of the most parsimonious hypothesis of phylogenetic relationships between the families Prochilodontidae and Curimatidae and within the Curimatidae (see Vari, 1983, for a discussion of synapomorphies for the Prochilodontidae). Numbered synapomorphies correspond to text.

retrieved from the classification, that hypothesis is discussed in detail in the following section and is presented visually in Figure 44.

Characters pertinent to phylogenetic reconstructions at the subgeneric levels are not typically be discussed unless they represent homoplasies found at both the generic and/or suprageneric levels on the one hand, and at subgeneric levels on the other. Exceptions are made for those unique synapomorphies that are pertinent to the hypotheses of species level relationships advanced by Vari for *Curimatopsis* (1982a) and *Potamorhina* (1984a), and which are in some instances reiterated or even expanded in this study.

Subsequent to the reconstruction of the most parsimonious hypothesis of phylogenetic relationships among the genera within the Curimatidae, I discuss the distribution of homoplasious characters, those derived attributes with an incongruent distribution on the cladogram (Figure 44). The discussion deals with the two types of homoplasies indicated by the final phylogeny. The first class involves derived characters that are common to two subunits of the family which are not each other's closest relatives. The second group consists of evidently identical derived characters that occur both within a subunit of the Curimatidae and in some characiform outgroup. The discussion of the homoplasies in conjunction with the phylogenetic reconstruction provides the basis for the evaluation of the efficacy of previous classificatory schemes as indicators of the phylogenetic history of the components of the family, that is its suprageneric groupings and genera as recognized in this study. Convergent characters are also evaluated in terms of whether they represent innovative or reductive attributes, and relative to the degree of congruence in those attributes within subunits of the Curimatidae.

The most parsimonious hypothesis incorporating the previously described synapomorphies, including homoplasies, is presented in Figure 44. This hypothesis was first derived by manual construction. Its parsimony was confirmed by use of David L. Swofford's (1985) numeric computer algorithm PAUP (Phylogenetic Analysis Using Parsimony), version 2.4. Synapomorphies unique to lineages recognized as genera in this study were not included in the analysis except in the case of genera with components that shared derived features with another generic or suprageneric clade within the Curimatidae.

The data on 49 discretely variable polarized features with two to four character states was analyzed using the branchandbound option of PAUP, guaranteed to find the most parsimonious trees. The analysis resulted in fifteen equally parsimonious trees with consistency indices of 0.825. These trees had identical topologies other than for the sequence of the genera *Curimatella, Cyphocharax, Steindachnerina,* and *Pseudocurimata.* Since those taxa form a terminal multichotomy, these fifteen trees are identical in terms of the phylogenetic hypothesis that they represent, and equivalent to the scheme of relationships in Figure 44. Characters are numbered sequentially from earlier to later dichotomies, simplifying the vizualization of character distribution, and allowing cross-referencinge of character descriptions and text discussions. The numbering of characters in the following text and in "Character Description and Analysis" corresponds to the numbered synapomorphies of Figure 44.

Characters pertinent to the species level phylogenetic reconstruction in *Curimatopsis* are sequentially identified alphabetically within the discussions of that genus and in Figure 45, but are not included in Figure 44. These form a separate character set.

MONOPHYLY OF THE CURIMATIDAE AND PROCHILODONTIDAE CLADE

Vari (1983:47) advanced eleven synapomorphies supporting the hypothesis that the Prochilodontidae is the sister group to the Curimatidae. These are listed below. Numbers 3, 9, 10, and 11 were discussed in detail by Vari (1983), to which the reader is referred for additional information. For the remaining synapomorphies, additional description and outgroup comparison may be found herein under "Character Description and Analysis."

1. Reorientation of the dorsal process of the fourth epibranchial anteriorly with its resultant extension over the dorsal surface of the fourth infrapharyngobranchial (Figures 5-13).
2. Anterodorsal expansion of the cartilaginous fifth epibranchial, its attachment to the posterodorsal margin of the fourth epibranchial, and the resultant encirclement by those elements of the fifth efferent branchial artery (Figures 5, 6, 8-11).
3. Large sac-like muscular epibranchial organ that extends dorsal to the medial elements of the dorsal portions of the gill arches (Vari, 1983:21-24).
4. Conversion of the plesiomorphously flat fourth upper pharyngeal tooth plate into a curved ossification that is wrapped around the ventral, lateral, and medial surfaces of the fourth infrapharyngobranchial (Figures 5, 6, 8-16).
5. Reduction or loss of dentition on the ventral surface of the fifth upper pharygneal tooth plate (Figures 5, 7-11).
6. Reduction or loss of an ossified first basibranchial.
7. Absence of dentition on the dorsal surface of the fifth ceratobranchial (Figures 25, 27).
8. Anteromedially directed process on the ventral surface of the fourth ceratobranchial.
9. Distinct posteroventrally aligned flange on the lateral surface of the opercle or a further derived condition of that process (Vari, 1983:29-30).
10. Increase in the depth and width of the fossa for the scaphium resulting in the interconnections of the fossa with the lateral occipital foramen laterally, and the interior of the cranium anteriorly (Vari, 1983:38-41, fig. 34).
11. 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. The exoccipital consequently forms a cover laterally for the the anterolateral surface of the scaphium (Vari, 1983:38–41, fig. 33).

The following additional derived characters shared by and uniting the Curimatidae and Prochilodontidae were discovered during this study. Additional description can be found under relevant sections of "Character Description and Analysis."

12. Constriction of the complex formed by the fourth infrapharyngobranchial and fourth upper pharyngeal tooth plate, resulting in a convex lateral margin to those conjoined elements (Figures 15, 16).
13. Expansion and restructuring of the uncinate process of the third epibranchial into an anterior process overlying the line of articulation between the third infrapharyngobranchial and third epibranchial (Figure 19).
14. Subdivision of the anterior articular surface of the third epibranchial, with the expansion and reorientation of the medial portion of the articulation into a medially directed ossified process extending along a matching groove on the the anterodorsal portion of the fourth infrapharyngobranchial (Figures 5, 6, 8–11, 19).
15. Expansion of the posterolateral portion of the third infrapharyngobranchial into a distinct dorsal flange (Figures 5, 6, 8–11).

As noted by Vari (1983:54–55) the phylogenetic hypothesis of a sister group relationship between the Curimatidae and Prochilodontidae agrees, partly or totally, with the classifications proposed by Günther (1864), Boulenger (1904), Regan (1911), Eigenmann (1917), Gregory and Conrad (1938), and Géry (1977b). All those authors included the majority of the taxa that are today considered to form the Curimatidae and Prochilodontidae in more encompassing groupings, along with taxa with which they are not closely related (Vari, 1983:54–55 for a more indepth discussion). Roberts (1973), in a significant shift from those earlier classifications, proposed that the relationships of the Prochilodontidae lies with the Anostomidae or the lineage formed by the Anostomidae and Chilodontidae rather than with the Curimatidae. Synapomorphies 12 to 15 discovered during this study, provide additional support for the hypothesis of the sister group relationship between the Curimatidae and Prochilodontidae. Those synapomorphies along with the shared derived characters proposed previously by Vari (1983) (SYNAPOMORPHIES 1–11) are incongruent with Roberts' (1973) hypothesis of a closer phylogenetic association of the Prochilodontidae with the Anostomidae, or with the group formed by the Anostomidae and Childontidae rather than with the Curimatidae.

MONOPHYLY AND INTRAFAMILIAL RELATIONSHIPS OF THE FAMILY CURIMATIDAE

In a previous publication Vari (1983:48) noted that the Curimatidae was the least derived family among the taxa under discussion (Curimatidae, Prochilodontidae, Anostomidae, and Chilodontidae) in terms of number of synapomorphies (ten) found. The ten synapomorphies found in that study (Vari, 1983) for the Curimatidae are listed below. Of these, synapomorphies 17, 22, 24, and 25 were discussed in detail by Vari (1983) and are not further detailed within this paper. Additional discussion of the remaining synapomorphies may be found under "Character Description and Analysis."

16. Absence of dentition on the dentary and premaxilla.
17. Possession of a third posttemporal fossa bordered solely by the epioccipital (Vari, 1983:37–38).
18. Expansion of the anteroventral portion of the third hypobranchial into a vertical flange with anterior and posterior processes (Figures 23–24).
19. Absence of an ossified first basibranchial (Figure 25).
20. Posteroventral expansion of fifth upper pharyngeal tooth plate into curved, convoluted process (Figures 5, 7, 11).
21. Secondary posterodorsal, cartilage capped process on the palatine which contacts a comparable process on the ventral wing of the lateral ethmoid (Figure 40).
22. Cartilage-capped articular process along the ventral edge of the ventral wing of the lateral ethmoid that articulates with the palatine (Vari, 1983:26–27, fig. 25).
23. Horizontal shelf on the medial surface of the metapterygoid.
24. Large cartilaginous ethmoid block and widened mesethmoid (Vari, 1983, figs. 36, 37).
25. Enlarged lagenar capsule (Vari, 1983:41).

Nine additional synapomorphies for the Curimatidae were discovered during this study (see also descriptions under "Character Description and Analysis"). They are as follows:

26. Ventral ridge extending from posterior of anteroventral articular surface of fourth epibranchial along ventral surface of the main body of that element (Figure 5).
27. Anterior reorientation of the primary axis of the dorsal process of the fourth epibranchial beyond the condition in the Prochilodontidae (Figures 5, 7–11).
28. Longitudinal ridges on the dorsal surface of the fourth ceratobranchial (Figure 26).
29. Dorsal convexity of the fifth ceratobranchial.
30. Transverse expansion of the fifth ceratobranchial both medial and lateral of the line between the anterior and posterolateral cartilage bodies (Figure 27B,C).
31. Presence of a well developed cord-like ligament running from the ventral hypohyal between the medial branchiostegal rays and extending along a groove on the midventral surface of the urohyal (Figure 32).
32. Extension of the urohyal posteriorly beyond the point

where the medial branchiostegal rays diverge laterally (secondarily shortened in *Curimata* and the clade consisting of *Steindachnerina, Pseudocurimata, Curimatella,* and *Cyphocharax* (see discussion under "Hyoid Arch")).

33. Anterolateral expansion of the portions of the first to third branchiostegal rays proximate to the hyoid arch, and the resulting overlap of the articulation of the second branchiostegal with the anterior ceratohyal by the anterior portion of the third branchiostegal.
34. Possession of a discrete ligamentous band, with a restricted area of attachment on the vomer, joining the neurocranium and the mesopterygoid.

As noted in the discussion of the "Opercular Aparatus," the form of the opercle and subopercle may represent additional synapomorphies for the family, but were not included here due to problems with non-arbitrary quantification .

The genera *Anodus* and *Eigenmannina* have traditionally been placed in the Curimatidae (e.g., Fernández-Yépez, 1948) or associated in an unspecified manner with that family (e.g., Eigenmann, 1917) as a consequence of their common lack of jaw dentition. This character, unique to *Anodus, Eigenmannina,* and adults of the Curimatidae among characiforms, both New and Old World, was presumably the basis for the original description of three species of curimatids in *Anodus* (*Anodus latior* Spix = *Potamorhina latior, Anodus ciliatus* Müller and Troschel = *Psectrogaster ciliata,* and *Anodus troschelii* Günther = *Pseudocurimata troschelii*). Roberts (1974), in a significant shift, proposed that *Anodus* and *Eigenmannina* (considered congeneric by Roberts, 1974) were members of the Hemiodontidae, and not closely related to to Curimatidae. Subsequently, Géry (1977b:239) commented upon the overall similarity of hemiodontids, *Anodus,* and *Eigenmannina,* and noted Roberts' (1974) publication in a footnote, but did not otherwise comment on the relationships of the different taxa. More recently, Géry (1984:357) has retained the "Anodins" (*Anodus* and *Eigenmannina*) in a broadly defined Curimatidae that does not form a monophyletic assemblage, and which he delimits from his "Hemiodins" (= Hemiodontidae). Although Géry (1984) noted that "The Anodins [*Anodus* and *Eigenmannina*] bear many resemblances to the Hemiodins," he neither provided any reason for his rejection of Roberts' (1974) hypothesis, nor did he elaborate on his continued alignment of *Anodus* and *Eigenmannina* with the Curimatidae.

The attributes listed by Roberts (1974:429) as justification for the inclusion of *Anodus* and *Eigenmannina* in the Hemiodontidae were an amalgam of three classes of characters. A number are synapomorphies for the Curimatidae (sensu stricto) (e.g., the cartilaginous articular surfaces between the palatine and the lateral ethmoid) that do define that family and serve to distinguish it from *Anodus* and *Eigenmannina,* but do not provide any insight into the phylogenetic position of those two genera to either the Curimatidae (sensu stricto) or the Hemiodontidae. The second group of features are shared primitive characters common to the Hemiodontidae, *Anodus,* and *Eigenmannina* (e.g., moderate coiling of the intestine), and which also occur in other groups of characiforms but are found in a derived condition in the Curimatidae. Such plesiomorphies are not useful in determining whether these three taxa form a monophyletic unit, or their possible phyletic associations with the Curimatidae. The third class of characters are shared derived modifications common to the Hemiodontidae, *Anodus,* and *Eigenmannina,* but which are not typical of the Curimatidae. Characters of that class cited by Roberts (1974) include the increased number of vertebrae, and the fusion of the first and second hypurals into a single ossification autogenous from the remainder of the hypural fan. Such characters are appropriately used as indicators of relationship and support Roberts' (1974) hypothesis that *Anodus* and *Eigenmannina* are aligned with the Hemiodontidae.

A more indepth evaluation of the placement of *Anodus* and *Eigenmannina* within the Hemiodontidae and a more rigorous definition of that family based on shared derived characters are both outside the scope of this study. The results of this study are, however, congruent with the hypothesis that *Anodus* and *Eigenmannina* are not closely related to the Curimatidae. Those genera share the synapomorphies noted above indicating that they are aligned phyletically with the Hemiodontidae. Furthermore those two genera lack the vast majority of the numerous hypothesized synapomorphies for the clade consisting of the Prochilodontidae and Curimatidae (SYNAPOMORPHIES 1–15), and the shared derived characters that delimit the Curimatidae (SYNAPOMORPHIES 16–34). The continued retention of *Anodus* and *Eigenmannina* in the Curimatidae would consequently require a hypothesis of secondary loss of nearly all of the derived characters in those two genera. That factor in combination with some of the characters cited by Roberts (1974) (see paragraph above) refute the implicit hypothesis of a close phyletic relationship of *Anodus* and *Eigenmannina* with the Curimatidae as advanced by Géry (1984).

The scheme of hypothesized phylogenetic relationships within the Curimatidae (Figure 44) has a basal pinnate form. The first dichotomy is between the clade consisting of the five species of *Curimatopsis* and the lineage formed by *Potamorhina, Curimata, Psectrogaster, Steindachnerina, Pseudocurimata, Curimatella,* and *Cyphocharax.*

Curimatopsis

Vari (1982a), in a revisionary study of *Curimatopsis,* advanced eight synapomorphies that served to delimit the four then-known species in the genus. These shared derived characters are also common to an additional species, *C. myersi,* that was described subsequently (Vari, 1982b). The five species of *Curimatopsis* occur in the Orinoco, Amazonas, and Paraguay rivers, and in some rivers of the Atlantic slopes of the Guyanas (see Vari, 1982a,b for details on those distributions). The derived characters advanced as synapomorphies for *Curimatopsis* by Vari (1982a) are as follows:

35. Expansion of the neural and haemal spines of the two posterior free preural centra into transversely flattened plates in the males.
36. Presence of basal spurs on the middle caudal-fin rays in the males.
37. Expansion of the penultimate principal caudal-fin ray of the lower lobe of the caudal fin in the males.
38. Ventral reorientation of the ventralmost ray of the upper caudal fin lobe.
39. Ventral expansion of the metapterygoid and the consequent reduction in the relative size of the metapterygoid-quadrate fenestra (Figure 42A).
40. Reduction to a single pair of uroneurals.
41. Absence of an ossified antorbital.
42. Reduction in the relative sizes of the supraorbital and the sixth infraorbital (dermosphenotic).

These synapomorphies are here supplemented by additional derived characters that also delimit the clade formed by the five species of *Curimatopsis* including *C. myersi*:

43. Oblique angle of articulation between the third infrapharyngobranchial and third epibranchial (Figure 15).
44. Very oblique angle of articulation between the second infrapharyngobranchial and second epibranchial, and the associated expansion of the second infrapharyngobranchial posterolaterally (Figure 15).
45. Possession of narrow rather than broad flanges along the ventrolateral margins of the urohyal.
46. Lack of a laterosensory canal segment in the first infraorbital.
47. Restructuring of the premaxilla into a very slender ossification.
48. Enlarged paddle-shaped body of the maxilla (Figure 38A).
49. Reduction of the ethmo-palatine cartilage to a relatively small body at the tip of the premaxilla (Figure 40A).
50. Reduction in the degree of scale poring of the laterosensory canal system of the body.

An additional possible synapomorphy for the members of *Curimatopsis* is the relatively elongate urohyal extending distinctly beyond the point of lateral divergence of the branchiostegal rays (see discussion under "Hyoid Arch").

Vari (1982a:10) proposed a phylogenetic scheme for the four species of *Curimatopsis* recognized in that study. As mentioned previously, an additional species (*C. myersi*) from the Río Paraguay basin was discovered and subsequently described (Vari, 1982b). The phylogenetic scheme for the expanded *Curimatopsis* is presented in Figure 45. Vari (1982a) discussed the following synapomorphies shared by *Curimatopsis macrolepis* and *C. microlepis*:

A. Lengthening of the postorbital portion of the head.
B. Terminal, upturned mouth with the lower jaw overlapping the anterior margin of the upper.

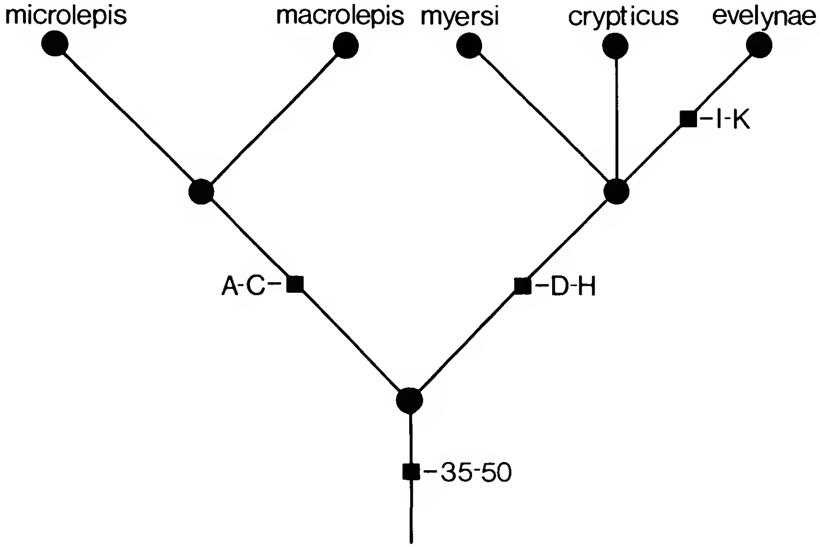

FIGURE 45.—Cladogram of the most parsimonious hypothesis of relationships within the genus *Curimatopsis*. Numbered and lettered synapomorphies correspond to text.

During the course of this analysis those two synapomorphies have been supplemented by an additional character that was not discussed by Vari (1982a):

C. Expansion of the anteroventral portion of the posttemporal and the lengthening of the segment of the laterosensory canal associated with the region of the bone.

The anteroventral region of the posttemporal is relatively small and has a short laterosensory canal segment in the Prochilodontidae, other species of *Curimatopsis*, and other genera of the Curimatidae. Given the unique nature of the expansion of that region of the bone in *C. microlepis* and *C. macrolepis* among curimatids, that correlation is hypothesized to be a synapomorphy for those two species. Similarly the elongation of the associated laterosensory canal segment in that region of the posttemporal is also hypothesized as synapomorphous for those species (SYNAPOMORPHY C).

The clade consisting of *Curimatopsis evelynae*, *C. crypticus*, and *C. myersi* is defined by three characters previously proposed by Vari (1982a):

D. Pronounced expansion of the penultimate principal ray of the lower lobe of the caudal fin in males.
E. Possession of a hypural 2 that is separate from the fused $PU_1 + U_1$, but fused to hypural 1.
F. Contact in the males of hypural 3 with the fused hypural 1 and 2, and the development posteriorly of interdigitations between those elements.

Additional synapomorphies for that clade are as follows:

G. Absence of an ossified sixth infraorbital (IO_6).
H. Laterally expanded longitudinal flanges on the midlateral surface of the posterior two free preural centra and the fused $PU_1 + U_1$.

Autapomorphies for *Curimatopsis evelynae* discovered since Vari (1982a) are primarily reductive, and given the small adult body size of the species may be the consequence of a paedomorphic process. These characters, which were not discussed by Vari (1982a), are as follows:

I. Reduction in the degree of ossification of the laterosensory canals in the second infraorbital.
J. Reduction in the degree of ossification of the laterosensory canals in the fourth infraorbital.
K. Absence of an ossified suprapreopercle.

Ossified laterosensory canal segments in the second and fourth infraorbitals and the ossification of the laterosensory canal above the preopercle as a separate supraperopercle are generalized for all other curimatids. Synapomorphies I, J, and K are consequently considered autapomorphous for *C. evelynae*.

Autapomorphies for the remaining *Curimatopsis* species have not been discovered, nor have characters been discovered that allow us to advance a hypothesis of sister species relationships within the trichotomy formed by *C. evelynae*, *C. crypticus*, and *C. myersi*.

Potamorhina, Curimata, Psectrogaster, Steindachnerina, Pseudocurimata, Curimatella, and *Cyphocharax*

These genera form a clade defined by thirteen synapomorphies:

51. Medial bony spur extending posteroventrally from the medial surface of the main body of the fourth epibranchial.
52. Pronounced anterior reorientation of the dorsal process of the fourth epibranchial beyond the condition in either the Prochilodontidae or *Curimatopsis* (Figures 7–11).
53. Anterior bony spur extending forward from the main body of the fourth epibranchial. That process serves as the area of attachment for the ligament extending between the third and fourth epibranchials (Figures 8, 10, 11, 13, 14).
54. Posterior lengthening of the fifth upper pharyngeal tooth plate, and the reduction of the dentition associated with that ossification (Figures 6–11).
55. Transversely subdivided posterior articular cartilage on the third infrapharyngobranchial (Figures 8, 10, 11).
56. Reduction or elimination of the gap between the articular cartilages on the anterior margin of the second hypobranchial (Figure 22B–D).
57. Enlarged ventral process on the fourth ceratobranchial that serves as a point of attachment for ligamentous tissues associated with the ventral aorta (present in *Potamorhina*, *Curimata*, and *Psectrogaster*; secondarily lost (SYNAPOMORPHY 93, below) in *Steindachnerina*, *Pseudocurimata*, *Curimatella*, and *Cyphocharax*).
58. Expansion of the portion of the ligamentum primordiale proximate to the A_1 portion of the Adductor Mandibulae muscle, either with or without an included cartilage body.
59. Opposing articular facets on the premaxilla and maxilla at their points of contact.
60. Expanded posterodorsal process of the main body of the maxilla (Figure 38B).
61. Sigmoid dorsal margin of the dentary (Figure 39B).
62. Subdivision of the articular cartilage of the palatine into an anterior portion contacting the ethmopalatine cartilage and vomer, and a posterior section with a dorsal articular surface that contacts the ventral articular process of the lateral ethmoid (Figure 40B).
63. Band-like ligament between the neurocranium and suspensorium with a discrete area of attachment to both the vomer and the mesopterygoid.

The large number of synapomorphies for this clade represent major restructurings of the gill arches, jaws, and associated soft tissues relative to the state of those systems in *Curimatopsis*. These perhaps reflect the increased specialization for a microphagous diet in the species of *Potamorhina*, *Curimata*, *Psectrogaster*, *Steindachnerina*, *Pseudocurimata*, *Curimatella*, and *Cyphocharax*. These modifications involve a number of systems which undergo further modifications at less inclusive levels of universality within the family. These independent evolutionary histories lead me to deal with these synapomorphies as thirteen independent features rather than attempting to arbitrarily group them as a reduced number of composite characters.

The lineage defined by characters 51-63 is, in turn, divisible into two monophyletic groups: one consisting of the species of the genus *Potamorhina*, the other formed by the genera *Curimata, Psectrogaster, Steindachnerina, Pseudocurimata, Curimatella*, and *Cyphocharax*.

Potamorhina

The genus *Potamorhina* consists of five relatively large-bodied species. *Potamorhina laticeps* is limited to the Lago Maracaibo basin. *P. squamoralevis* inhabits the Río Paraguay basin. *Potamorhina latior* and *P. pristigaster* are endemic to the Río Amazonas system. *P. altamazonica* is common to the Río Amazonas system and the Río Orinoco (see Vari, 1984a, for further details on species distribution). *Potamorhina* was defined by Vari (1984a:13) on the basis of six synapomorphies, listed below. Synapomorphy 68 was described in detail by Vari (1984a) and is not discussed elsewhere in this paper. The remainder are described herein under "Character Description and Analysis":

64. Horizontal lengthening of the anterodorsally aligned dorsal process of the fourth epibranchial and its associated distal cartilage (Figure 10).
65. Contact of the distal cartilage of the fourth epibranchial with the cartilage of the uncinate process of the third epibranchial (Figure 10).
66. Horizontal elongation of the fourth basibranchial, fourth ceratobranchial and the complex formed by the fourth infrapharyngobranchial and fourth upper pharyngeal tooth plate (Figure 10).
67. Elaboration of the laterosensory canal system in the sixth infraorbital from a tripartite system into one with four or more branches (Figure 36C).
68. Presence of two or three unbranched rays and 11-16 branched rays in the anal fin (Vari, 1984a:7).
69. Possession of 85-110 pored lateral line scales from the supracleithrum to the hypural joint.

The additional synapomorphies for the species of *Potamorhina* discovered during this study are as follows:

70. Lengthening of the fifth epibranchial into a long anteriorly tapering body (Figure 10).
71. Subdivision of the articular process on the uncinate process of the first epibranchial (Figure 21).
72. Posterior elongation of infraorbitals four and five (IO_4 and IO_5) and the associated lengthening of the posterior horizontal laterosensory canal segment in the fourth infraorbital.
73. Greater posterior development and more oblique orientation of the opercle.
74. Posterior development of the interopercle into a large triangular plate between the preopercle, subopercle, and opercle.

An additional possible synapomorphy for the members of *Potamorhina* is the relatively elongate urohyal extending distinctly beyond the point of lateral divergence of the branchiostegal rays (see discussion under "Hyoid Arch").

Vari (1984a:13) advanced a hypothesis of relationships among the five recognized species of *Potamorhina*. Only one additional character pertinent to that hypothesis was uncovered during this study and it is congruent with the previously proposed phylogenetic scheme for and within *Potamorhina*, (see Vari, 1984a:4-11, fig. 6).

The additional derived character discovered during this study is an autapomorphy for *Potamorhina pristigaster*. This feature involves the marked shift posteriorly of the fourth and fifth infraorbitals and the consequent more acute angle between the axes of the laterosensory canal segments of those elements. As discussed previously, this shift is somewhat similar in overall appearence to that in species of *Steindachnerina, Pseudocurimata, Curimatella*, and *Cyphocharax* (SYNAPOMORPHY 95). The morphological plan of these elements in *Potamorhina pristigaster* is a consequence of a posterior shift in the position of the elements relative to the orbit, and differs in various details from the condition in the cited genera. In light of those differences and within the context of the overall most parsimonious hypothesis of relationships, the state in *P. pristigaster* is considered non-homologous with that in *Steindachnerina, Pseudocurimata, Curimatella*, and *Cyphocharax*.

Curimata, Psectrogaster, Steindachnerina, Pseudocurimata, Curimatella, and *Cyphocharax*

The sister lineage to *Potamorhina* is a clade consisting of six genera: *Curimata, Psectrogaster, Steindachnerina, Pseudocurimata, Curimatella*, and *Cyphocharax*. That lineage is delimited by three shared derived characters:

75. Elimination of the gap between the anterior articular cartilages along the anterior margin of the second hypobranchial with the fusion of the cartilage bodies into a single mass (Figure 22C-D).
76. Development of a buccopharyngeal complex consisting of three longitudinal fleshy folds on the roof of the oral cavity, or a further derived elaboration of that complex.
77. Well developed ridge on the medial surface of the metapterygoid (Figures 41, 42).

The clade delimited by synapomorphies 75–77 contains two subunits defined by less universal derived characters. These are *Curimata* on the one hand, and the clade consisting of *Psectrogaster, Steindachnerina, Curimatella,* and *Cypocharax* on the other.

Curimata

The genus *Curimata* is a distinctive group of moderate to large sized species inhabiting the Río Magdalena, the Río Orinoco, the rivers of the Atlantic slopes of the Guyanas, some of the rivers of northeastern Brazil, and the Amazon basin. *Curimata* is characterized by six synapomorphies:

78. Ontogenetic reconfiguration of the medial spur on the fourth epibranchial into a ventrally expanded process contacting the medial margins of the fifth upper pharyngeal tooth plate (Figures 7, 8).
79. Development of a median shelf on the dorsal margin of the spur of the fourth epibranchial, and the associated pronounced fenestration of that spur (Figure 8).
80. Medial shift of the medial spur and ventral articular processes of the fourth epibranchial, and of the associated fifth upper pharyngeal tooth plate (Figure 14).
81. Reduction or loss of the first infrapharyngobranchial.
82. Elaboration of the three primary folds of the buccopharyngeal complex into large ventral flaps, and the development of numerous secondary parallel folds on the roof of the buccal cavity (Figure 28).
83. Thickened anteromedial portion of the metapterygoid (Figure 42D).

An additional possible synapomorphy for the members of *Curimata* is the relatively short urohyal extending only to the point of lateral divergence of the branchiostegal rays. The morphology of that system may represent a secondary reversal from the condition in a more inclusive clade (see discussion under "Hyoid Arch").

Psectrogaster, Steindachnerina, Pseudocurimata, Curimatella, and *Cyphocharax*

These genera, comprising the sister group to *Curimata,* share two derived characters:

84. Possession of a discrete cartilage embedded in an aponeurotic covering within the expanded basal portion of the ligamentum primordiale (Figure 37).
85. Posteroventral expansion of the mesopterygoid into an elongate process extending into and partially or totally subdividing the metapterygoid-quadrate fenestra (Figure 41B).

Synapomorphies 84 and 85 unite two clades: that recognized herein as *Psectrogaster,* and the lineage consisting of *Steindachnerina, Curimatella, Pseudocurimata,* and *Cyphocharax.*

Psectrogaster

The species of *Psectrogaster* are distributed within the Río Orinoco, Essequibo River, Amazon basin, some of the rivers of northeastern Brazil, and the Río Paraguay system. *Psectrogaster* species have in common the following seven synapomorphies:

86. Posterior elongation of the medial spur on the main body of the fourth epibranchial (Figure 9).
87. Elongation and distal twisting of the fifth upper pharyngeal tooth plate (Figure 9).
88. Well developed longitudinal ridge on the ventral surface of the third epibranchial.
89. Well developed longitudinal ridge on the ventral surface of the second epibranchial.
90. Distinct flange on the dorsal surface of the second infrapharyngobranchial that overlies the anteromedial portion of the third infrapharyngobranchial.
91. Distinct longitudinal ridge on the ventral surface of the first epibranchial.
92. Longitudinal ridge on the dorsal surface of the third ceratobranchial.

An additional possible synapomorphy for the members of *Psectrogaster* is the relatively elongate urohyal extending distinctly beyond the point of lateral divergence of the branchiostegal rays (see discussion under "Hyoid Arch").

Steindachnerina, Pseudocurimata, Curimatella, and *Cyphocharax*

The lineage consisting of these genera is characterized by four synapomorphies:

93. Secondary loss of the enlarged ventral process on the fourth ceratobranchial that is found in *Potamorhina, Curimata,* and *Psectrogaster* (SYNAPOMORPHY 57).
94. Presence of a basihyal tooth plate.
95. Reorientation of the canals in the fourth and fifth infraorbitals (IO_4 and IO_5) with the consequent reduction in the angle of the primary axes between the laterosensory canal segments in those ossifications (Figure 35C).
96. Reduction of the laterosensory canal system in the sixth infraorbital (IO_6) to a single tube extending between the fifth infraorbital and pterotic laterosensory canal segments (Figure 36 D).

An additional character possibly synapomorphous for the lineage consisting of *Steindachnerina, Pseudocurimata, Curimatella,* and *Cyphocharax* involves the form of the urohyal. These genera are characterized by a relatively short urohyal that reaches posteriorly to the point of lateral divergence of the branchiostegal rays. Three alternative, equally parsimonious, hypotheses exist to explain the occurrence of the derived condition, the more elongate urohyal, in *Curimatopsis, Potamorhina,* and *Curimata.* One of these alternatives involves the derived secondary reduction of the urohyal in the clade consisting of *Steindachnerina, Pseudocurimata, Curimatella,* and *Cyphocharax* (the other alternatives are discussed under "Hyoid Arch").

It is not possible to resolve the hypothesis of relationships among the remaining genera in the family (*Steindachnerina, Pseudocurimata, Curimatella,* and *Cyphocharax*) on the basis of the characters uncovered during this study. Synapomorphous characters do, however, permit the definition of three of these groups (*Steindachnerina, Pseudocurimata,* and *Curimatella*) as individual monophyletic units. The remaining genus, *Cyphocharax,* is not delimited by any known derived characters, and it is thus possible that some or all of its component taxa may actually be more closely related to *Steindachnerina, Pseudocurimata,* or *Curimatella,* or some combination of these genera than to the remaining species of *Cyphocharax* (see also discussion of *Cyphocharax,* below). These four remaining recognized genera are discussed sequentially, with the order of presentation not indicative of any underlying hypothesis of relationships.

Steindachnerina

Steindachnerina is the largest genus in the Curimatidae, with a geographic distribution covering much of the known range of the family in South America east of the Andes together with a single species (*S. atratoensis*) to the west of the Andean cordilleras in the Río Atrato system of Colombia. The hypothesized synapomorphies for the species of *Steindachnerina* are as follows:

97. Ventral and dorsal ridges on the lateral surface of the second infrapharyngobranchial that bracket the anteromedial portion of the third infrapharyngobranchial.
98. Expansion of the cartilaginous portion of the first infrapharyngobranchial and its contact with the second infrapharyngobranchial.
99. Attachment of the ligament between the second and third hypobranchials to a distinct anterior process on the anterolateral surface of the ventral process of the third hypobranchial (Figure 24).
100. Lateral expansion of the anterior portion of the basihyal and associated basihyal tooth plate (Figure 33B).

Pseudocurimata

The species of *Pseudocurimata* are limited to the trans-Andean drainages of northwestern South America from the Río Atrato of Colombia to the Río Chira of northern Peru. This distribution is nearly totally allopatric to the remainder of the family other than for the partial overlap of the range of *P. lineopunctata* with that of *Steindachnerina atratoensis* in the Río Atrato system. Synapomorphies for the genus are as follows:

101. Expansion of the portion of the second hypobranchial proximate to the third basibranchial and the fission of the articular cartilage on the anterior and medial surfaces of the second hypobranchial (Figure 22D).
102. Posterior shift of the point of interdigitation of the first proximal pterygiophore of the dorsal fin to between the fifth and sixth, or sixth and seventh, neural spines (Figure43B–C).
103. Pronounced reduction or complete loss of the second set of uroneurals.

Curimatella

The relatively few species (probably six or seven) of *Curimatella* occur in the ríos Orinoco, Amazonas, Essequibo, São Francisco, and the La Plata basin. The genus is distinguished by the presence of the following synapomorphy:

104. Layer of scales extending across the lobes of the caudal fin.

Cyphocharax

Taxa assigned to *Cyphocharax* in this study are widely distributed through nearly the entire range of the family Curimatidae with the exception of the trans-Andean rivers to the west and south of the Río Magdalena of Colombia that are inhabited by species of *Pseudocurimata. Cyphocharax* species are also absent in the rivers of northeastern Brazil.

The characters discovered during this study have not included any synapomorphies congruent with a hypothesis of the monophyly of *Cyphocharax.* The combination of that lack of any defining characters for *Cyphocharax* and the multichotomy that exists between that genus, *Curimatella, Pseudocurimata,* and *Steindachnerina* leaves open the possibility that some components of *Cyphocharax* may be more closely related to one or more of the other genera in the multichotomy than to the remaining species of *Cyphocharax.*

Although *Cyphocharax* is not readily definable on the basis of derived characters, there are some recognizable assemblages within that genus that are to varying degrees phyletically and phenetically distinguishable and may represent monophyletic subunits of the genus. The largest of these involves eleven nominal taxa characterized by a distinctive dark midlateral spot on the caudal peduncle, such as is typical for *Cyphocharax spilurus.* Other nominal taxa of the *C. spilurus* species group sharing this evidently derived character are *C. spiluropsis, C. gillii, C. surinamensis, C. helleri, C. stigmaturus, C. esperanzae, C. ucayalensis, C. vandellii, C. esperanzae pijpersi,* and

C. spilota (see Table 2 for information on authors and original generic placement of these taxa).

A second assemblage consists of curimatids of relatively small adult body size, the first described being *C. saladensis*. The *C. saladensis* species group consists of that species, *C. punctata*, and *C. vanderi* all of which share a reduction in the extent of the poring in the lateral line, a less developed laterosensory canal system of the head, in particular of the canal segments in the infraorbitals, and a general reduction in the degree of development of various cranial sculpturing. These paedomorphic characters cannot be evaluated here as to the particular heterochronic process that has resulted in these results, but are potentially derived characters that unite these species into a monophyletic group (see Weitzman and Vari, 1988, for further discussion of reductive characters and of their utility in phylogenetic reconstructions).

Another major assemblage, the *Cyphocarex gilberti* species group, includes species sharing overall distinctive pigmentation patterns, including a rhomboidal caudal pigmentation pattern in juveniles and random body spotting, which are possibly derived. The nominal members of the *C. gilberti* species group are *C. gilberti, C. voga, C. albula, C. grandocule, C. santacatarinae*, and *C. modesta* (see Table 2 for authors and original generic assignments). *Cyphocharax platana* and *C. nagellii*, in turn, are phenetically very similar species with distinctive body forms and having contiguous ranges in the La Plata and upper Río Paraná systems respectively. These may be sister species. Groupings among the remaining nominal *Cyphocharax* species are not as apparent at this time.

Cyphocharax Fowler (1906) as utilized in this study is considered to have four synonyms: *Xyrocharax* Fowler (1913b), *Hemicurimata* Myers (1929), *Curimatoides* Fowler (1940), and *Cruxentina* Fernández-Yépez (1948). *Cyphocharax, Xyrocharax, Hemicurimata*, and *Curimatoides* all have type species which either represent the same species or very closely related species, all of which belong to the *C. spilurus* species group. *Xyrocharax* has not been utilized by authors other than Fowler (1913b), whereas *Curimatoides* is evidently based on a single aberrant individual lacking an adipose dorsal fin.

Given the lack of resolution of the phylogeny at this point and the clumping of the vast majority of the type species of the available nominal genera in a small subunit of this assemblage it is most conservative to recognize a single genus for this questionably monophyletic assemblage. The alternative, the recognition of all nominal available genera, or an intermediate number of taxa would necessitate the creation of a series of new genera for the different species groupings described above for which generic names have not been previously proposed. Such an elaboration of the supraspecific taxonomy within this assemblage is considered inappropriate given the phylogenetic uncertainties involving interrelationships among the species united within *Cyphocharax* at this time, and in light of the absence of any advantages to such a more complex taxonomic scheme.

Unassigned

One feature, involving the elongation of the urohyal, was assigned a synapomorphy number for inclusion in the PAUP analysis and for discussion purposes (see "Urohyal" and "Convergent Characters"), but does not appear on the cladogram (Figure 44). The reason is that three interpretations of its behavior on the cladogram, each involving three independent derivations or losses, are equally parsimonious. The feature is as follows:

105. Elongation of the urohyal past the point of lateral divergence of the branchiostegal rays in *Curimatopsis, Potamorhina*, and *Psectrogaster*.

Convergent Characters

The hypothesis of phylogenetic relationships within the family Curimatidae proposed in this study is the most parsimonious derivable from those characters showing discrete variability within the family when considered in the context of the available information on character homology, polarity, and distribution. The utilization of the principle of simplicity (parismony), as the criterion to evaluate the preferability of alternative hypotheses has been the subject of some controversy (e.g., Felsenstein and Sober, 1986). However, this procedure, the acceptance of the hypothesis that requires the fewest ad hoc assumptions, is still preferable (Beatty and Fink, 1979; Eldredge and Cracraft, 1980; Wiley, 1981). I recognize, nonetheless, that evolutionary processes are not necessarily parsimonious, with the result that evident homoplasies are features of most phylogenetic schemes including the one proposed in this study.

The hypothesis of phylogenetic relationships described herein includes features, from diverse body systems, that have a phyletic distribution incongruent with the final most parsimonious phylogenetic scheme. Such incongruent derived characters, homoplasies, will be evaluated here within two contexts. The first framework deals solely with the phylogenetic distribution of the characters regardless of the type of character involved. Do the homoplasies under consideration characterize two or more independent sublineages within the Curimatidae (convergences internal to the Curimatidae), or do they represent the independent acquisition of the character in question both in a subunit of the Curimatidae and in some characiform outgroup (convergences external to the Curimatidae)? Those comparisons serve to emphasize the phyletic patterns of homoplasy and focus attention on those clades that evidently have independently undergone congruent patterns of convergent evolution. Admittedly the distinction between internal and external homoplasies is based on arbitrary taxonomic limits, but serves nonetheless to convey a general sense of the phyletic proximity of the clades involved in the comparisons.

One can alternatively discuss homoplasies in terms of their innovative or reductive natures (Weitzman and Fink, 1985) outside of a strictly phyletic context. Innovative characters, having "additional features beyond those present in the outgroups" (Weitzman and Fink, 1985:10), are a consequence of changes in peramorphic processes and most commonly represent terminal additions in overall developmental sequences. Reductive characters in contradistinction involve the reduction or loss of a feature present in the outgroups and may result from a number of different paedomorphic developmental changes resulting from progenesis, neoteny, and post-displacement. The analysis of common patterns of reductive homoplasies within a phylogentic scheme derived from multiple characters, innovative and reductive, congruent and incongruent, permits an evaluation of the utility of at least some reductive characters as indicators of phylogenetic relationship.

Since the homoplasies to be discussed within these two contexts (phyletic, and innovative versus reductive) are the same, they will only be detailed in the first set of discussions, those on phyletic distribution. Homoplasies in that discussion are divided between internal homoplasies and external homoplasies, and are listed sequentially by synapomorphy number. These synapomorphies will also be discussed in the context of reductive versus innovative homoplasies.

The homoplasies found in two or more subunits of the Curimatidae (internal homoplasies) and their phylogenetic distributions are as follows, listed by synapomorphy number (see also "Character Description and Analysis" and "Synapomorphy List and Phylogenetic Reconstruction"):

21. Subdivided articular processes on the uncinate process of the first epibranchial in *Potamorhina* and the lineage consisting of *Curimata incompta, C. cyprinoides, C. copei, C. schomburgkii, C. edentulus, C. planirostris, C. kneri, C. mivartii, C. cerasina, C. aspera, C. simulata, C. cisandina, C. alleni,* and two undescribed species of *Curimata.*
28. Elaboration of the buccopharyngeal complex in *Curimata* species and the majority of *Steindachnerina* species.
46. Absence of a laterosensory canal segment in the first infraorbital in all *Curimatopsis* species, *Steindachnerina binotata, Cyphocharax gillii, C. saladensis, C. punctata,* and *C. vanderi.* This reduction also occurs in various characiform outgroups but not in the proximate outgroups Prochilodontidae, Anostomidae, and Chilodontidae.
50. Reduction in the degree of poring of the laterosensory canal system on the body in *Curimatopsis* and in three species of *Cyphocharax* (*vanderi, punctata,* and *saladensis*); also reduced in some other characiforms, but not in the proximate outgroups to the Curimatidae.
69. High number of lateral-line scales in *Cyphocharax abramoides* and in the species of *Potamorhina.*
88. Well developed ventral longitudinal ridges along the ventral surface of the third epibranchial in *Curimata aspera, C. simulata, C. cerasina,* and all *Psectrogaster* species.
89. Well developed ventral longitudinal ridges along the ventral surface of the second epibranchial in *Curimata mivartii, C. aspera, C. simulata, C. cerasina, C. cisandina, C. alleni,* two undescribed *Curimata* species, and all species of *Psectrogaster.*
90. Distinct flange on the anterodorsal surface of the second infrapharyngobranchial in *Psectrogaster* (see also discussion of Synapomorphy 97 and under "Third Epibranchial").
91. Longitudinal ridge along the ventral surface of the first epibranchial in *Psectrogaster* and in two species of *Curimata.*
92. Longitudinal ridge along the dorsal surface of the third ceratobranchial in *Psectrogaster* and in *Curimata mivartii, C. aspera, C. simulata, C. cerasina, C. alleni,* and two undescribed species of *Curimata.*
94. Presence of a basihyal tooth plate in a subset of species of *Curimata* and in the vast majority of the species in the lineage consisting of *Steindachnerina, Pseudocurimata, Curimatella,* and *Cyphocharax.*
97. Distinct flange on the anterodorsal surface of the second infrapharyngobranchial in *Steindachnerina* (see also 91, above, and discussion under "Third Epibranchial").
102. Posterior position of the interdigitation of the first proximal pterygiophore of the dorsal fin with the proximate neural spines in *Curimata ocellata, C. semitaenitata,* and all *Pseudocurimata* species (also present in some outgroups, see "Supraneurals").
105. Elongation of the urohyal past the point of lateral divergence of the branchiostegal rays in *Curimatopsis, Potamorhina,* and *Psectrogaster.* Three alternative, equally parsimonious hypothesis exist (see discussion under 'Urohyal'). The first is that a lengthened urohyal is synapomorphous for all species of the Curimatidae and is secondarily independently shortened in *Curimata* and the lineage consisting of *Steindachnerina, Pseudocurimata, Curimatella,* and *Cyphocharax.* The elongation may also be acquired at the level of the Curimatidae, with a reduction in the clade consisting of *Curimata, Psectrogaster, Steindachnerina, Pseudocurimata, Curimatella,* and *Cyphocharax,* with a secondary lengthening in *Psectrogaster.* Finally, the elongation may have been independently acquired within each of the three lineages, *Curimatopsis, Potamorhina,* and *Psectrogaster.* The feature was not used in the cladogram because of the several possible interpretations of its distribution.

As can be seen in the above listing, a number of generic and subgeneric subunits possess characters homoplasious relative to the overall most parsimonious hypothesis of intrafamilial relationships. Nonetheless, relatively few patterns of repeated homoplasy among those taxa were discovered during the course of this study. Reductive features of the laterosensory canal system of the head and body are common to *Curimatopsis* species and a subunit of *Cyphocharax* (SYNAPOMORPHIES 46 and 50, see also discussion in next section). *Psectrogaster* and subunits of *Curimata* of varying levels of inclusiveness also share several convergences involving longitudinal ridges on various gill arch elements (SYNAPOMORPHIES 89, 92 at one level, and 89, 91 at another). The differing levels of inclusiveness at which these convergences are common in those genera, along with overall parsimony considerations indicate that these are homoplasious rather than homologous features.

The second subset of homoplasies are derived synapomorphies occurring in a subunit of the Curimatidae and also in a characiform outgroup (external homoplasies). These are as follows:

16. Absence of jaw teeth in all members of the Curimatidae, and in *Anodus* and *Eigenmannina* of the Hemiodontidae.
39. Reduction in the size of the metapterygoid-quadrate fenestra as a consequence of the ventral expansion of the metapterygoid in *Curimatopsis*, and in the Chilodontidae.
41. Absence of an ossified antorbital in *Curimatopsis* in the Curimatidae, and in the African characid *Lepidarchus adonis*.
100. Expansion of the basihyal and basihyal tooth plate in *Steindachnerina*, and in the Prochilodontidae.
104. Sheet of scales across the lobes of the caudal fin in *Curimatella*, and in the genus *Leporellus* in the Anostomidae.

Synapomorphies 46, 50, and 102, homoplasious within the Curimatidae, are also synapomorphous for some lineages outside of that family. Only synapomorphy 102 is homoplasiously present in proximate outgroups of the Curimatidae.

The above listing of external homoplasies should not be considered exhaustive since it is not feasible to carry out outgroup comparisons against the entire spectrum of characiform outgroups. These comparisons have for practicality been focused on the proximate sister groups to the Curimatidae, the Prochilodontidae, Anostomidae, and Chilodontidae.

An alternative way to look at the above attributes is to ask whether they are innovative or reductive, and whether these classes of homoplasies demonstrate a meaningful pattern relative to the arrived at phylogenetic hypothesis. The innovative characters in the previous listings having a homoplasious distribution internal to the Curimatidae are numbers 28, 69, 88–92, 94, 102, and 105. The innovative characters in the previous listing having a homoplasious distribution external to the Curimatidae are 39, 100, and 104.

The innovative homoplasies are common to some members of the Curimatidae and a diversity of outgroups. These do not, however, demonstrate any patterns that would support alternative hypotheses of relationships. This lack of congruence makes it unfruitful to speculate on common underlying factors resulting in these homoplasies.

The reductive homoplasies, internal to the Curimatidae, uncovered during this study are synapomorphies 46 and 50. Those external to the Curimatidae are synapomorphies 16 and 41.

Reductive characters and their utility in phylogenetic reconstructions in fishes in general and characiforms in particular have been the subject of discussions by various authors (e.g., Weitzman and Fink, 1983; Weitzman and Vari, 1988). As noted by those authors, paedomorphic features cannot be a priori distinguished from primitive states in the absence of information on phylogenetic relationships derived from multiple character systems involving innovative and reductive apomorphies. The bulk of the characters used by different authors in advancing hypotheses of relationships in characiforms involve external characters. In the Curimatidae the external reductive features most often used for those purposes have involved the extent of development of the laterosensory canal system, in particular the degree of scale poring associated with the lateral line on the body.

The use of a reduction in the degree of poring on the lateral line to distinguish a species at the supraspecific level within the Curimatidae was first advanced by Steindachner (1876) who proposed *Curimatopsis* as a subgenus of *Curimata* in his description of *C. macrolepis*, a species that has scale poring developed only on the anterior portion of the laterosensory system of the body. That character was, in turn, used by Eigenmann and Eigenmann (1889b) as part of their definition of *Curimatopsis* as a genus and in their description of *Curimatopsis microlepis*, by Ahl (1931) when proposing *Curimatopsis macrocephalus*, and by Géry (1964a) for his *Curimatopsis evelynae*. Other authors who have also used *Curimatopsis* for species with incompletely pored lateral lines are Meinken (1933) in his description of *Curimatopsis saladensis* and Ahl (1934) when he described *Curimatopsis maculatus*. Vari (1982a) redefined *Curimatopsis* on the basis of a number of derived innovative characters and described *C. crypticus*, a species with an incompletely pored lateral line. That attribute also characterized *C. myersi*, subsequently described by Vari (1982b). Both *Curimata vanderi* Britski (1980) and *C. punctata* Vari and Nijssen (1986) have lateral line scale poring limited to the anterior portion of the body, but were not placed by their authors in *Curimatopsis*.

The nominal species with incomplete poring of the laterosensory canal system of the body fall into two distinct groups, those assignable to *Curimatopsis* as defined by Vari (1982a) and in this study (*C. macrolepis*, *C. microlepis*, *C. microcephalus* (= *C. macrolepis*), *C. evelynae*, *C. crypticus*, and *C. myersi*), and those assigned herein to *Cyphocharax* (*C. saladensis*, *C. maculatus*, *C. vanderi*, and *C. punctata*). The

Curimatopsis species are definable by a number of unique innovative synapomorphies (see "Synapomorphy List and Phylogenetic Reconstruction"). *Cyphocharax*, although not itself delimited by any unique characters, does share numerous synapomorphies at different levels of universality with *Potamorhina, Curimata, Psectrogaster, Steindachnerina, Curimatella*, and *Pseudocurimata*; characters not found in *Curimatopsis* species. Thus the data overwhelmingly indicate that the clade recognized as *Curimatopsis* and the assemblage of species of *Cyphocharax* with incomplete poring of the lateral line are not closely related to each other (*Curimatopsis maculatus* Ahl, which has an incomplete lateral line, is based on a juvenile of a *Cyphocharax* species that has a fully pored lateral line as an adult). The reduced development of portions of the laterosensory canal system of the body in the two assemblages is considered homoplasious, although constituting a synapomorphy for each of the assemblages at lower levels of universality. A similar situation involves the absence of the laterosensory canal segment in the first infraorbital; a reduction that characterizes the species having the reduced poring of the lateral line and in addition *Steindachnerina binotata*. Again the absence of that canal segment is judged to be homoplasious within the family given the overall most parsimonious hypothesis of relationships within the Curimatidae. That character is nonetheless an evident synapomorphy for *Curimatopsis* on the one hand, and the assemblage formed by *Cyphocharax saladensis, C. vanderi*, and *C. punctata* on the other, and is an autapomorphy for *Steindachnerina binotata*.

Reductive characters present problems relative to their utility in the generation of phylogenetic hypotheses. Some authors (e.g., Hecht and Edwards, 1977) have noted the potential difficulties in determining homologies when losses or reductions are being studied since it is not possible to critically compare a character that is absent. Similarly Weitzman and Vari (1988) discussed the difficulties in discriminating paedomorphic features from primitive characters in the absence of a phylogenetic framework. Those problems are well exemplified by the reductions in the laterosensory canal segments noted above, and the need for phylogenetic studies to evaluate such patterns emphasized by Weitzman and Vari is well demonstrated. By focusing on a single reductive body system, the reduced lateral line poring, Meinken (1933) and Ahl (1934) aligned their nominal species (*C. saladensis* and *C. maculata* respectively) with *Curimatopsis* (sensu stricto). The phylogenetic hypothesis based on a more extensive set of characters, internal and external, indicates in contradistinction that those reductions were independently achieved in those two species and *Curimatopsis*.

Weitzman and Vari (1988) also discussed the correlation between paedomorphic features and reductions in relative body sizes. Although none of the curimatid species with reductive characters fits the size limit for miniatures proposed in that study, those authors noted that miniaturization must be dealt with as a relative concept. Miniatures must be judged relative to the body sizes of their immediate outgroups. Within that definition, some of the curimatids with reductive features could perhaps be considered miniatures. Four of the *Curimatopsis* species (*macrolepis, evelynae, myersi*, and *crypticus*) are all among the smallest species of curimatids, being much smaller than any species of the Prochilodontidae, which is the sister group to the Curimatidae. Species of *Curimatopsis* are also of smaller maximum body size than the species of their sequential proximate sister groups within the Curimatidae: *Potamorhina*, whose species achieve 205–265 mm SL; *Curimata*, whose members reach 112–235 mm SL; and *Psectrogaster*, the species of which grow to 130–210 mm SL.

Curimatopsis is definable on the basis of sixteen synapomorphies. Five of these (SYNAPOMORPHIES 40, 41, 42, 46, and 50) are reductive, two involving losses of autogenous ossifications (the second set of uroneurals, SYNAPOMORPHY 40, and the antorbital, SYNAPOMORPHY 41). The other three reductive synapomorphies for the genus involve reductions in the degree of development of the laterosensory canal systems of the head and body, along with a reduction or loss of some of the dermal ossifications associated with that sensory system. Although *Curimatopsis* species do not as adults approach the standard lengths of members of the Prochilodontidae or proximate clades to that genus within the Curimatidae, there is nonetheless more than a two-fold range between the standard lengths of the largest examined individuals of *C. evelynae* (40.1 mm SL) and *C. microlepis* (99.4 mm SL). Across the range of lengths within the genus there is a correlation between body size and the degree of expression of various reductive, apparently paedomorphic features. *Curimatopsis microlepis* and *C. macrolepis* which achieve standard lengths of 99.4 mm and 60.6 mm respectively do not demonstrate any reductive features beyond those general for the genus. The species of the sister group to the clade formed by those genera, the lineage consisting of *C. evelynae, C. crypticus*, and *C. myersi*, range in size from 40.1 mm to 48.7 mm SL. That clade is characterized in part by an additional reductive feature, the absence of an ossified sixth infraorbital (*Curimatopis* SYNAPOMORPHY G). The trend to smaller adult body sizes is most pronounced in *Curimatopsis evelynae*, which also autapomorphously possesses a further series of reductive characters involving the laterosensory canal system (*Curimatopsis* SYNAPOMORPHIES I, J, H). These losses are among those "typical" for miniatures according to Weitzman and Vari (1988), and the progressive increase in the number of paedomorphic features would be expected if there is a correlation between a reduction in body size and a truncation of developmental sequences. Further studies are necessary to determine whether the evident correlation between reduced size and an increase in apparently paedomorphic features that is found in *Curimatopsis* is a general pattern across the Characiformes.

The concept of miniatures might also be applied to at least some of the *Cyphocharax* species with reductive features.

Again these are species smaller than the other members of the genus and proximate outgroups, although one species, *Cyphocharax saladensis*, does achieve relatively large body sizes (58.3 mm SL). A more definitive statement on possible paedomorphosis in *Cyphocharax* must await the proposal of a phylogenetic hypothesis for those members of the genus of reduced body size.

Comparisons with Previous Classifications

A variety of alternative classificatory schemes have been proposed for, and applied to, the species of the Curimatidae. One extreme in this century was advanced by Eigenmann (1910:420–422) who recognized only seven genera for the known species of Curimatidae, exclusive of *Anodus* and *Eigenmannina*. At the opposite extreme, less than four decades later Fernández-Yépez (1948), describing 17 new genera, recognized 29 genera. Fowler (1906, 1913b, 1940, 1941) independently advanced a number of genera that have been inconsistently recognized since their proposal.

The complexity of the alternative previous classifications of the Curimatidae makes it inefficient to discuss comparative merits and problems of each of those systems. Rather I will only discuss those two arrangements that have been most widely utilized: Eigenmann (1910), and Fernández-Yépez (1948). Independently and in common, these demonstrate problems typical of the diverse classificatory schemes proposed for the Curimatidae.

Eigenmann's (1910) classification consisted of the following: one large genus, *Curimatus*, containing about 71% of the 66 species then recognized in the family; four genera (*Psectrogaster*, *Curimatella*, *Curimatopsis*, and *Semitapicis*) with two to eight nominal species; and two monotypic genera (*Potamorhina* and *Gasterotomus*). Among the genera recognized by Eigenmann (1910) with two or more species, only one, *Curimatopsis*, reflected a monophyletic unit in the phylogeny proposed in the present study. *Psectrogaster* as defined herein was divided by Eigenmann (1910) between that genus (sensu stricto) and *Curimatus* (*C. isognathus* and *C. rutiloides*). Similarly *Curimatella* of Eigenmann (1910) agrees relatively well although not completely with the concept of that genus proposed in this study, but *Curimatus dorsalis* Eigenmann and Eigenmann was retained in *Curimatus* by Eigenmann (1910), whereas currently available data indicate that its closest relatives are the *Curimatella* species of Eigenmann's (1910) classification.

Eigenmann's (1910) *Curimatus*, his most inclusive genus, has components that are now assignable to nearly all the curimatid lineages described herein, including the following genera (with Eigenmann's, 1910, species): *Cyphocharax* (*Curimatus spilurus*, *C. gillii*); *Curimatella* (*Curimatus dorsalis*, *C. leucostictus*); *Steindachnerina* (*Curimatus nasus*, *C. conspersa*); *Pseudocurimata* (*Curimatus troschelii*, *C. brevipes*); *Curimata* (*Curimatus aspera*, *C. mivartii*); and *Psectrogaster* (*Curimatus rutiloides*, *C. isognathus*). Reference to Figure 44 shows that *Curimatus* in the sense of Eigenmann (1910) is thus scattered across the phylogeny proposed here, and so does not form a monophyletic assemblage. Also, components placed by Eigenmann (1910) in other nominal genera (e.g., *Curimatella* (sensu stricto), *Psectrogaster* (sensu stricto), *Semitapicis* (in part)) would have to be returned to *Curimatus* as defined by Eigenmann in order for that genus to be monophyletic.

This situation exemplifies one of the most common consequence of classifications predicated primarily on concepts of external differences. The taxa with some externally obvious, often derived, characters were separated in their own genera. As a result the remaining species were left in an assemblage definable only by the absence of the distinctive features of the excluded taxa. Such taxa consisting of residual species were in most instances non-monophyletic, or if monophyletic, could not be recognized as such from data then available.

Fernández-Yépez (1948) drastically subdivided the Curimatidae into 27 genera (not including *Anodus* and *Eigenmannina*) of which ten were monotypic. That high percentage of monotypy and the large number of genera with small numbers of species would make generic level comparisons between that system and the results of this study tedious and confusing. As a consequence the best framework to evaluate Fernández-Yépez's (1948) classification is to compare the distribution of species within his classification with the groupings arrived at in the present study.

No lineages were found to be common to the two schemes of relationship, with drastic differences between them occurring in most instances. A case by case comparison would again be tedious but several examples will be given to provide a sense of the differences. The genus *Potamorhina* of the present study, a lineage well corroborated by multiple synapomorphies, is subdivided between the tribes Potamorhini and Curimatini under Fernández-Yépez's (1948) system. Both of those taxa, in turn, contained species assigned to all of the other lineages recognized herein, with the exception of *Curimatopsis*. *Curimata*, as defined herein, was scattered across eight genera in Fernández-Yépez's scheme, with individual *Curimata* species aligned by that author with species considered to belong to *Cyphocharax*, *Steindachnerina*, *Psectrogaster*, and *Curimatella* in this paper. Furthermore the individual lineages containing species of *Curimata* did not form a discrete subunit in Fernández-Yépez's (1948) phylogenetic scheme. Comparable problems with Fernández-Yépez's (1948) "phylogenetic tree" exist relative to each of the other lineages recognized in this study. Thus the congruence of Fernández-Yépez's (1948) classification with the phylogeny proposed herein is judged to be minimal.

To a large extent the cited problems appear to be the result of Fernández-Yépez's (1948) dependence on a few characters as the basis for his classification. One of the most significant of those features was the degree of development of various prepelvic, postpelvic, and predorsal angles in the body walls, with that being supplemented by characters involving scalation on the caudal fin rays, relative fin position, mouth form and position, and degree of development of the laterosensory canal system on the body. Many of those noted characters do constitute synapomorphies at some levels of universality and thus are potentially useful in generating phylogenetic hypotheses. Nonetheless they also demonstrate a notable degree of convergence within the Curimatidae in the context of the phylogeny proposed herein. Such convergence can only be detected by the examination of a broader spectrum of internal and external characters than those utilized by Fernández-Yépez (1948) and other authors. This problem is best exemplified by the convergencies in the laterosensory canal system reductions that have been discussed in the previous sections. Above and beyond questions of character homology and homoplasy, Fernández-Yépez's (1948) classification also demonstrates the weaknesses already commented on relative to the Eigenmann (1910) scheme — the separation of phenetically externally distinctive taxa into their own monotypic genera, leaving non-monophyletic residual amalgams of externally generalized species typically recognized as genera.

Although both authors used primarily external features as the basis for their classifications, the noted problems in their taxonomic schemes are not a consequence of the reduced utility of external characters in phylogenetic reconstructions, but rather an outgrowth of the methodologies utilized. The problems noted above for the classifications of Eigenmann (1910) and Fernández-Yépez (1948) are, in turn, typical of the classifications proposed by other authors who have also dealt with the family (e.g., Fowler, 1975).

Resumo

A família Curimatidae consiste de mais de 120 espécies nominais que habitam uma ampla série de ecossistemas de água doce neotropicais, variando desde os lagos e rios de curso lento das terras baixas até os riachos de curso mais rápido das elevações médias ao longo do sopé dos Andes e das terras altas do escudo das Guianas e do escudo do Brasil. Curimatídeos ocorrem a oeste e ao norte dos Andes nos rios das vertentes do Pacífico, desde o sul da Costa Rica até a norte do Peru, e nas drenagens do Caribe no noroeste da América do Sul, incluindo os sistemas do rio Atrato, rio Magdalena e lago Maracaibo. Os maiores números de espécies de curimatídeos ocorrem nas vertentes atlânticas da América do Sul, desde o rio Orinoco, passando pela bacia Amazônica e os rios costeiros das Guianas, Brasil, Uruguai e Argentina, até ao sul de Buenos Aires.

Classificacões prévias da família não foram baseadas em hipóteses de relações evolutivas dentro da família. Em lugar disso estas propuseram novos gêneros e subgêneros com base em graus de similaridade ou diferença e, assim mesmo, usando somente caracteres externos. A "árvore filogenética" formulada por Fernández-Yépez (1948) é uma representação direta de sua chave dicotômica para os gêneros da família e não de um verdadeiro esquema filogenético. Como consequência desses e outros problemas, muitas das unidades taxonômicas situadas acima do nível de espécie reconhecidas em classificões prévias não representam agrupamentos naturais. Os estudos relatados neste trabalho foram realizados tendo em vista a formulação de uma hipótese, baseada em caracteres derivados distintos, quanto às relações filogenéticas a nível supra-específico dentro da família Curimatidae.

O esqueleto e outros sistemas anatômicos das espécies da família Curimatidae foram estudados com o fim de se investigar a hipótese de que esta é uma subunidade da ordem Characiformes, e também de se propor uma hipótese quanto às relações filogenéticas dentro da família. Sinapomorfias associadas com o aparelho branquial, complexo buco-faringeano, arco hióide, antorbital, infra-orbitais, aparelho opercular, "ligamentum primordiale," maxilas, arco palatino e neurocrânio são congruentes com a hipótese de que a família é uma linhagem monofilética. Caracteres adicionais num subgrupo desses sistemas são congruentes com a hipótese proposta por Vari (1983) quanto a Curimatidae e Prochilodontidae serem grupos-irmãos. A posse em comun de caracteres derivados nos sistemas corporais citados anteriormente, assim como no complexo hipural, nos raios da nadadeira caudal e na coluna vertebral definem subunidades naturais dos Curimatidae. Esses caracteres apoiam uma hipótese filogenética com quatro dicotomias sequenciais e uma politomia terminal. Sete linhagens, reconhecidas como gêneros (*Curimatopsis, Potamorhina, Curimata, Psectrogaster, Steindachnerina, Pseudocurimata,* e *Curimatella*), são consideradas monofiléticas com base na posse em comum de caracteres derivados. Não foram encontrados caracteres derivados únicos que definam *Cyphocharax,* o oitavo gênero reconhecido.

A hipótese para relações filogenéticas intra-familiares obtida neste estudo é incongruente, em diferentes graus, com os esquemas de classificação propostos por Eigenmann & Eigenmann (1889b), Eigenmann (1910), Fowler (1975), e Géry (1977b). Existem numerosas diferenças, em todos os níveis taxonômicos, entre o esquema de interrelações proposto neste estudo e a "árvore filogenética" apresentada por Fernández-Yépez (1948). A transferência, proposta pela primeira vez por Roberts (1974), dos gêneros *Anodus* Spix e *Eigenmannina* Fowler, tradicionalmente incluídos nos Curimatidae, para os Hemiodontidae, é uma mudança congruente com os resultados obtidos por Vari (1983), estando de acordo com a distribuição de vários caracteres adicionais considerados como derivados descobertos durante o presente estudo.

Oito gêneros: *Curimatopsis* Steindachner (1876), *Potamorhina* Cope (1878), *Curimata* Bosc (1817), *Psectrogaster* Eigenmann & Eigenmann (1889a), *Steindachnerina* Fowler (1906), *Pseudocurimata* Fernández-Yépez (1948), *Curimatella* Eigenmann & Eigenmann (1889b) e *Cyphocharax* Fowler (1906) são reconhecidos na família. *Curimatichthys* Fernández-Yépez (1948) é considerado um sinônimo de *Curimatopsis. Potamorhina* é redefinida de maneira a incluir *Gasterotomus* Eigenmann (1910), *Gasterostomus* Fernández-Yépez (1948), *Suprasinelepichthys* Fernández-Yépez (1948), e *Potamorrhina* Braga & Azpelicueta (1983). *Curimata* Bosc (1817) tem nove sinônimos juniores: *Semitapicis* Eigenmann & Eigenmann (1889b), *Peltapleura* Fowler (1906), *Acuticurimata* Fowler (1941), *Allenina* Fernández-Yépez (1948), *Lambepiedra* Fernández-Yépez (1948), *Bitricarinatra* Fernández-Yépez (1948), *Bondichthys* Whitley (1953), *Stupens* Whitley (1954), e *Semitapiscis* Braga and Azpelicueta (1983). Três gêneros são incluídos em *Psectrogaster.* Estes são: *Pseudopsectrogaster* Fernández-Yépez

(1948), *Hamatichthys* Fernández-Yépez (1948) e *Semelcarinata* Fernández-Yépez (1948). *Rivasella* e *Curimatorbis*, ambos propostos por Fernández-Yépez (1948), são colocados como sinônimos de *Steindachnerina* Fowler (1906). *Curimatella* tem três sinônimos juniores: *Apolinarella*, *Walbaunina* e *Lepipinna*, todos de autoria de Fernández-Yépez (1948). *Cyphocharax* tem quatro sinônimos: *Xyrocharax* Fowler (1913b), *Hemicurimata* Myers (1929), *Curimatoides* Fowler (1940) e *Cruxentina* Fernández-Yépez (1948).

Caracteres homoplásicos em relação à filogenia proposta são discutidos em termos da sua distribuiçao dentro e fora da família Curimatidae e também quanto a serem caracteres inovadores ou redutivos.

Caracteres redutivos, envolvendo o grau de desenvolvimento do sistema de canais látero-sensoriais cefálicos e corporais presentes nas espécies de *Curimatopsis* e num grupo de espécies de *Cyphocharax*, revelaran-se convergentes. Estes caracteres pedomórficos são evidentemente uma consequência da miniaturização relativa dessas espécies em comparação com seus extra-grupos mais próximos.

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