RELATIONSHIPS OF THE NEON TETRAS, A GROUP OF SOUTH AMERICAN FRESHWATER FISHES (TELEOSTEI, CHARACIDAE), WITH COMMENTS ON THE PHYLOGENY OF NEW WORLD CHARACIFORMS

STANLEY H. WEITZMAN[1] and WILLIAM L. FINK[2]

CONTENTS

ABSTRACT. The history of the classification and the relationships of the American Characidae is reviewed in terms of phylogenetic principles. Current characid systematics is found unstable and unsatisfactory from typological and phylogenetic points of view. We predict that the classification of the American characids and that of all characiforms will be subject to much reinterpretation and rearrangement through future phylogenetic analyses.

The three known species of neon tetras are used as an example of phylogenetic analysis within the American Characidae. This analysis exemplifies the difficulties of an initial phylogenetic study of a taxon with many ill-defined subgroups.

These three species previously were placed in two characid subfamilies and three genera as follows: *Hyphessobrycon simulans*, the green neon, in the Tetragonopterinae; *Cheirodon axelrodi*, the cardinal tetra, and *Paracheirodon innesi*, the neon tetra, in the Cheirodontinae. Several synapomorphies were found to unite all three species, which are herein placed in *Paracheirodon*. The interrelationships among the three neon tetras are not resolved.

INTRODUCTION

The Characidae comprises the largest part of a group of freshwater fishes, the Characiformes, whose living representatives are endemic to Africa and South and Central America. American characids are found from southern Argentina and Chile in South America north to the Mexico-United States border area in North America. The greatest concentration of species occurs in the Amazon basin, the largest geographic area. There are fewer species to the north in the Orinoco basin and to the south in the Paraná-Paraguay river system. Still fewer species occur in the numerous smaller drainage basins in Central America and peripheral to these three large river systems in South America. By the latest account, Géry (1977: 13–16), the American part of the family consists of 12 "subfamilies" and about 700 species, excluding Serrasalminae and Characidiinae, both sometimes included within the Characidae. The phylogeny of these

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[1] National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

[2] Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138. Present address: Department of Biology and Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48104.

"subfamilies" and their relationships to other characiforms are poorly understood.

Systematists studying American characids owe much to the pioneering studies of Eigenmann and his students early in this century. The system of characid classification inaugurated by Eigenmann has formed the framework within which nearly all subsequent research has been done. But there are serious shortcomings with that system, acknowledged by Eigenmann (1917: 43–49), and in recent years there has been some movement toward a different approach to the problems recognized by Eigenmann. Current characid classification is neither phylogenetically nor typologically useful. In the following pages we reexamine the basis for traditional classification of the group, rooted in Eigenmann's concepts of systematic ichthyology, and discuss the approaches several more recent authors have brought to bear on the problem. We propose and discuss the implications of a phylogenetic approach to characid relationships, and present a phylogenetic analysis of a small but representative characid group, the neon tetras.

Many groups of characiforms, including the American characids, include species whose members are of very small size, 12 to 25 or 30 mm in standard length (SL). Many of these species exhibit paedomorphic features, such as reduction in the extent and surrounding ossification of the laterosensory system and reduction in tooth cusp number. The problems of attempting to recognize and diagnose genealogical lineages in a group where small size and reductive features are so common is also treated.

METHODS

The analysis used here is phylogenetic, basically that of Hennig (1966). Much discussion and some modification of Hennig's views have occurred since 1966. The reader is referred to Farris (1978, 1979), Cracraft and Eldredge (1979), Eldredge and Cracraft (1980), Hull (1980), and Wiley (1981), for reviews of recent theoretical and practical views regarding phylogenetic systematics and cladistics.

Counts and measurements follow Fink and Weitzman (1974) unless otherwise explained in the text. All measurements are given as a percent of standard length except those subunits of the head which are a percent of head length.

The synonymies are limited to the original descriptions, accounts of the discovery of the neon tetras, morphological and systematic reports, and aquarium literature accounts providing new name combinations. Most aquarium literature is not cited.

The following abbreviations are used for institutions:

ANSP—Academy of Natural Sciences of Philadelphia
BMNH—British Museum (Natural History), London
CAS—California Academy of Sciences, San Francisco [catalog numbers may read CAS(IUM), formerly of Indiana University, or CAS(SU), formerly of Stanford University]
EPA—Fundação de Amparo à Pesquisa do Estado de São Paulo, Expedição Permanente da Amazônia, São Paulo
FMNH—Field Museum of Natural History, Chicago
INPA—Instituto Nacional de Pesquisas da Amazonia, Manaus
MBUCV—Museo de Biologia, Instituto de Zoologia Tropical, Universidad Central de Venezuela, Caracas
MCZ—Museum of Comparative Zoology, Harvard University, Cambridge
MZUSP—Museu de Zoologia da Universidade de São Paulo, São Paulo
NRM—Naturhistoriska Riksmuseet, Stockholm
USNM—United States National Museum, the collections in the Division of Fishes, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Other abbreviations used are:

SL—Standard length
spms—specimens

The species and specimens other than neon tetras examined for this investigation are listed in Appendix 1. The neon tetras are listed in the species accounts.

In the lists of specimens examined, locality information follows the following format: the country is given first in its English form followed by the state, department, or district in the language of the country. This is followed by the specific locality.

SYSTEMATICS OF THE AMERICAN CHARACIDAE

The history of American characid systematics was summarized by Eigenmann (1917) and updated by Weitzman (1962). Since the latter paper appeared, classification within the family has been discussed by several authors, including Roberts (1973), Fink and Weitzman (1974), Rosen (1970, 1972), and Géry (1977). None of the authors subsequent to Eigenmann (1917) has been able to treat adequately the various problems brought forth in that seminal paper. As we will make clear below, we think that progress has been hindered by the kinds of systematic approaches that were employed. It would be useful at this point to summarize Eigenmann's comments, since he was particularly perceptive about aspects of evolution that interest systematic theorists today.

Eigenmann, in a series of papers published early in this century, greatly expanded our knowledge of the complexity of the characid fauna. He was the first author to consider to any appreciable extent the evolutionary relationships of the numerous genera of the American characids. In earlier papers, Eigenmann and his students followed the ichthyological standards of the day and proposed genera based on obvious differences among morphological features. Eigenmann (1914: 23) noted that many characid genera appear polyphyletic. The problem of generic and subfamily relationships came to be one of his primary concerns when he attempted a broad synthesis of his knowledge of American characiforms in 1917. Eigenmann clearly understood the differences between what are now called phylogenetic and grade concepts of classification. Eigenmann (1914: 23) stated: "We recognize two types of genera, one a group of closely related species, descended from a common ancestor and having certain distinguishing characters in common. . . . The other, a polyphyletic type, consists of species having a certain combination of definite characters in common which easily distinguish members of the genus, but which, instead of indicating a single ancestral line from which the species have diverged, are acquired possibly one at a time along distinct lines converging to a common definition. Sometimes the polyphyletic origin can be detected, sometimes not." Eigenmann (1917: 48) came to describe the genera of the Tetragonopterinae as "an interlacing fabric rather than a branching tree." Many of the characters utilized by Eigenmann and his students are those used traditionally as "generic characters" by ichthyologists working with other groups of fishes then and today. Despite Eigenmann's warnings of serious problems for the recognition of characiform genera based on these characters, most subsequent ichthyologists have continued to use this system of names, concepts, and categories for characids at the generic and subfamilial levels. We would here point out that we believe there is nothing inadequate or "wrong" with the characters used; rather, it is how they have been used and interpreted that has been and still remains the problem. Myers (*in* Eigenmann and Myers, 1929: 546) pointed out that "We do not yet have a key to the mensuration of phylogenetic differentiation in the tetragonopterid characins, and until we do it would seem the best course to follow the existing method [referring to the Eigenmann system of genera, subfamilies, and usage of characters]." Often more recent ichthyologists have tried to "fit" new species and genera into Eigenmann's system by a rigid use of Eigenmann's "generic characters" as set forth in "The American Characidae" (Eigenmann, 1917: 42). Since many of these newly discovered species did not "fit" well into the system, a proliferation of new generic names ensued. Examples include Schultz (1956) and Géry (1960a,b; 1963; 1965a,b; 1966a,b; 1977). In our opinion this procedure is now leading to problems in the usefulness of characid genera as either monophyletic or typological entities. A rigid use of certain characters as always significant at the generic level is producing chaos in the classification of characids.

Eigenmann (1915: 3 and 10–11) and Böhlke (1952: 794) pointed out the possible or probable polyphyly of the cheirodontine characids. This suggestion was further supported by Weitzman (1962: 5), Géry (1977: 543), Vari and Géry (1980: 80), and especially by Fink and Weitzman (1974: 1). Ellis (*in* Eigenmann, 1918: 135), in referring to the tetragonopterine genera *Hemigrammus* and *Hyphessobrycon*, stated the following: "It seems quite certain that these genera are of polyphyletic origin, that several sections have been and are arising independently from *Astyanax* and *Moenkhausia* and probably other genera. These genera (*Hemigrammus* and *Hyphessobrycon*) are conveniences rather than entities." We think these genera are no longer "conveniences." Their typological convenience is at an end because it often conflicts with information from additional characters and consequent ideas about relationships. For example, Böhlke (1955: 233–234), in a discussion of the relationships among some species of *Hemigrammus* and *Hyphessobrycon*, found an analysis of their relationships difficult and ambiguous. In that contribution Böhlke described a new species, *Hemigrammus mimus*, which, on the basis of characters employed by Ellis (*in* Eigenmann, 1918: 133–135) to define *Hemigrammus* and *Hyphessobrycon*, would have to be placed in *Hyphessobrycon*. In view of other characters, Böhlke placed the fish in *Hemigrammus*, predicting that it is most closely related to a known species of *Hemigrammus*. Thus, Böhlke refused to follow the traditional use of a character (presence of caudal-fin squamation) that always had been considered as having "generic value."

The first explicitly phylogenetic study of a characid group is that of Rosen (1972) on *Bramocharax*. He studied the relationships of the species and subspecies in the genus and compared them with species in the tetragonopterine genera *Astyanax*, *Moenkhausia*, *Hemigrammus*, *Deuterodon*, *Bryconamericus*, and *Hemibrycon*. Comparisons apparently were limited to these genera because of the similarity to them of the most primitive *Bramocharax* species. Rosen's conclusion, based on shared unique characters, was that *Bramocharax* is monophyletic and represents the sister group to some lineage within *Astyanax*. The similarity of primitive *Bramocharax* species to *Astyanax* species is so great that Rosen questioned the recognition of *Bramocharax* as distinct from *Astyanax*. Rosen left unanalyzed the implication of his study that *Astyanax* is paraphyletic when *Bramocharax* is recognized.

Roberts (1973) attempted an analysis of the relationships among three genera of presumed glandulocaudine characids of the Guayas basin in western Ecuador. He evaluated certain features on the basis of whether they were primitive, reductive, labile, or specialized. Although he did not define or use characters according to phylogenetic methodology, Roberts (1973: 512) emphasized that of his four categories, specialized characters "are most important in determining relationships." Specialized characters were defined as originating only once and "... incapable of having originated independently." Roberts noted that the generic classification in Eigenmann's "The American Characidae" is based largely on reductive and labile characters, which Roberts did not consider specialized according to his concepts. In his study Roberts came to the conclusion that none of the osteological characters that he examined could be used as evidence to support his original hypothesis that the "... Guayas glandulocaudins are an autochthonous monophyletic lineage and had *Bryconamericus*-like ancestors." He further concluded that these characters and many others found in characids are unlikely to be useful in studies of phylogenetic relationships because of their lability or their reductive nature. We suspect he came to this judgment because he assumed the species represented an autochthonous radiation without investigating the possible relationships of the three genera with other glandulocaudines outside the Guayas basin, and also because he did not investigate the characters he used in sufficient detail. Our primary criticism of Roberts' analysis is that he seems not to have considered the fact that "labile or reductive" characters may be indicative of monophyly at some taxonomic level even though they may not be significant at the levels under study.

Fink and Weitzman (1974: 4–5) discussed the traditional use of so-called "generic" characters, including lateral-line length, tooth-cusp morphology, procurrent caudal-fin rays, and caudal-fin squamation. Lateral-line length had traditionally been used to "recognize" *Odontostilbe* as different from *Cheirodon*. Fink and Weitzman found, however, that lateral-line length was variable in *Cheirodon dialepturus* Fink and Weitzman and *C. affinis* (Evermann and Goldsborough) to such an extent that in some populations of each species some individuals were "*Odontostilbe*" while others were "*Cheirodon*." Since lateral-line length was the only character which distinguished *Odontostilbe* from *Cheirodon*, the former name was synonymized with the latter. A similar approach was used with the other characters listed above, resulting in synonymizing of *Pseudocheirodon* and *Compsura* with *Cheirodon*. These actions were taken by Fink and Weitzman (1974) to eliminate clearly typological genera whose diagnostic features were no longer useful to pigeonhole characid species.

Subsequently Géry (1977: 554–555) suggested that this practice, if carried to its logical extreme, would result in "lumping" of all "tetragonoterine" genera into a single genus represented by the oldest available name, *Tetragonopterus*. Ulrey (1895) once did what Géry suggested. The species treated by Ulrey previously had been placed in six genera, with most of them in *Tetragonopterus*. Ulrey (1895: 262) cites the variability of the lateral line in given species as one of his reasons for an inclusive genus *Tetragonopterus* and therefore the doubtful significance of this "generic" character. By today's standards, this approach is an oversimplification of a complex problem. Reduction in pored lateral-line length could be variable in one species of a given monophyletic line but constant within another monophyletic line and therefore useful as a synapomorphy delineating that particular lineage. It may be that *Odontostilbe*, the type of which is the Peruvian *Cheirodon fugitiva* (Cope), might still be a recognizable, monophyletic genus. However, since the sole character upon which it was based has been shown to be invalid at the level at which it has been applied, recognition of *Odontostilbe* would require: (1) a detailed study of the species of *Cheirodon* possibly related to *C. fugitiva* to determine if there are characters which could define a monophyletic group; (2) a study of the phylogenetic relationships of all of the species currently placed in *Cheirodon* to determine if *Cheirodon* would be paraphyletic as a consequence of removing some species of *Cheirodon* to the genus *Odontostilbe.* Géry, *in* Vari and Géry (1980: 81), now seems to accept the reasons for not recognizing *Pseudocheirodon* and *Compsura.*

The most serious problem we now find with the work of Fink and Weitzman (1974) is its lack of rigorous analysis of relationships. Statements referring to "relationships" made by them are unsubstantiated by presentation of putative synapomorphies. For example, on page 25 they considered *Cheirodon terrabae* Bussing as "close to" *C. affinis,* but presented no evidence corroborating this hypothesis. They made a traditional assessment of the number of characters in common between these species but did not explicitly search for derived characters shared by them. This practice has been (and remains) the predominant method of assessing species relationships in ichthyology. It is a process which is logically flawed, and it does not necessarily lead to a stable classification.

To present a broad evaluation of the classification of neotropical characids as expressed in the current literature we must discuss the approach taken by Géry to characid systematics in a long series of papers (see bibliographies in Géry, 1972 and 1977). Géry has been the main proponent in recent years of the "classical" or "Eigenmann" system and much of his work has been recently summarized (Géry, 1977). Because of his efforts to preserve this system Géry has been forced into decisions which, to us, do not make good systematic sense. We cite the following two examples to illustrate the difficulties he encountered and to provide some insight into his rationale and the problems for characid classification that result.

Géry (1966b: 111–112) discussed population samples of a characid which were extremely similar to *Hemigrammus unilineatus* (Gill), a widespread and somewhat variable species of northern South America. In these population samples, all specimens examined had complete lateral lines rather than the reduced ("incomplete") lateral line of *H. unilineatus,* thus giving them the diagnostic feature of another genus, *Moenkhausia.* In his remarks on the situation Géry (1966: 111) stated: "We are thus faced with a form which differs from *H. unilineatus cayennensis*: (a) at the subspecific level (scarcely at the specific one) by a number of characters, and (b) at the generic level by one character, the completeness of the lateral line . . . . The validity of the genus *Moenkhausia* . . . may even be questioned, if the present form is considered as a mere variety of *H. unilineatus.*" Near the end of his discussion (p. 112) he stated: "The stability of the nomenclature of Characids [sic] therefore demands that the form here described as *Moenkhausia hemmigramoides* be considered as generically distinct from *Hemigrammus unilineatus,* even though the latter is probably derived from it by regression . . . . Needless to say, this is a compromise." Another example of Géry's systematic practice involves the work of Rosen (1972) on *Bramocharax,* cited above. In spite of Rosen's analysis of relationships of *Bramocharax* species and *Astyanax,* Géry (1977: 302 and 322) chose to recognize *Bramocharax* as a separate tribe, Bramocharacini, placing it "near" the tribe Acestrorhynchini, in the subfamily Characinae rather than in his Tetragonopterinae with *Astyanax.* Géry apparently wished to ignore the documented relationships of *Bramocharax* and stated (p. 302): "Between the two groups [Géry's Characini and Acestrorhynchini], or forming a linking ring with the Tetragonopterinae, is a curious fish, *Bramocharax* . . . in a separate tribe. It resembles an *Astyanax* but with a large characine type mouth and caniniform teeth (as well as pleuricuspid ones)." Géry's concepts of "relationship" clearly are not genealogical and his reference to a "linking ring" is a peculiar echo of the various quinarian taxonomic systems of the early 19th century.

We find Géry's taxonomy to be unacceptable. It is difficult to criticize Géry's work on the basis of a definitive approach to systematics because we are not sure of the nature of his goals and methods. Indeed, Géry has remarked to us personally that his work is not to be taken as an expression of phylogenetic relationships. We certainly agree with him on this point. The difficulty remains that in his papers Géry seems to be writing about relationships based on evolutionary descent, but the meaning of his statements about relationships escapes us. We consider that the price Géry is paying to preserve a traditional system is too high. Efforts to preserve a system which neither represents knowledge of phylogenetic relationships nor acts as a "sorting system," but which instead produces a proliferation of subjective, unsubstantiated judgments about some kinds of undefined "relationships" are counterproductive to efforts to provide a heuristic system for other comparative biologists.

We believe that a new analysis of characid systematics is necessary, one that holds a better promise of eventual systematic stability or which at least clearly defines the problems in any given taxon. For this purpose the phylogenetic approach seems equaled by no others (Farris, 1978; Eldredge, 1979; Wiley, 1981). Characiform phylogenetic analyses have already begun (Vari, 1979; Winterbottom, 1980; Fink and Fink, 1981), but efforts directed toward the American characiforms have so far been limited to Rosen (1972), Weitzman and Cruz (1981), Weitzman and Géry (1981), Vari (1982), Weitzman and Weitzman (1982), and Vari (1983).

A recurrent theme that appears in systematic works on neotropical characids is the difficulty of assessing relationships in the face of specializations accompanying small body size. Many of the "generic" characters discussed above (e.g., incompleteness of the lateral line, reduced caudal-fin squamation) are suspected of having appeared independently in numerous lineages. Myers (1958: 29) noted that a number of reductive evolutionary trends occur in the morphology of small characiforms (and many other small teleosts) with adult body lengths ranging from 10 to 25 mm. Myers attributed these trends to "neoteny." Weitzman (1962: 5–6) also discussed reductive evolution in characids, specifically with reference to osteological features. He warned that "loss of various parts of the laterosensory system, or parts of the skeleton, although providing good characters for identification, must be used with extreme care in the study of phyletic relationships of small fishes, since parallel loss is probably the rule rather than the exception." As noted by Fink (1982) such multiple evolutionary "reductions" amount to anomalies in character distributions in the context of cladograms, usually attributed to paedomorphosis. However, providing a process "explanation" to account for the phenomenon does not change the problems of how such traits may be used in phylogenetic analyses.

The fundamental issue is detecting single *vs.* multiple acquisition of similar morphologies, i.e., detection of synapomorphy *vs.* homoplasy. The only solution to the problem of which we are aware is detection of more derived characters which are congruent with the distribution of certain others, thus providing a basis for choice among competing hypotheses of relationships. Simply because certain traits are "reductive" does not mitigate their usefulness as part of a phylogenetic analysis. Nevertheless, it is wise to look at "reductive" characters very closely, especially when the data are contradictory. In some cases, several aspects of an organism's morphology may be modified by a single change in developmental timing. Hence, all these aspects could be considered a single character rather than several. Comparisons of developmental stages in the taxa where heterochrony is suspected with similar stages in appropriate outgroups often will allow one to determine whether or not, and to what extent, several traits may be "correlated." As will be evident in the present analysis, the greatest difficulty with this kind of analysis of characids is the lack of well-defined outgroups. For further discussion of models for analysis of ontogenetic processes, see Fink (1982).

IMPLICATIONS OF A PHYLOGENETIC CLASSIFICATION OF THE CHARACIFORMES

In a phylogenetic classification, the groups given names are based on shared derived characters and represent the most parsimonious arrangement of all the attributes of the organisms. In addition, a phylogenetic classification recognizes only complete sets of organisms and their complete subsets, which should represent monophyletic evolutionary lineages. In contrast, a phenetic or traditional "evolutionary" classification recognizes paraphyletic "groups" nomenclaturally. We emphasize here that paraphyletic groups, as incomplete sets, are neither maximally informative about the distribution of attributes of organisms, nor representative of the reality of phylogenetic evolution. Paraphyletic groups are subjective, artificial products of systematists' minds, as discussed by Fink (1979), among others.

The implications of this approach to the classification of the characid and characiform fishes (as well as all "fishes") are profound. Once our knowledge progresses to the point that we can discern lines of evolution within characiform groups, those lineages will be recognized nomenclaturally. It is highly likely, for example, that the family Characidae (*sensu* Greenwood *et al.*, 1966: 383) is a paraphyletic (or perhaps polyphyletic) assemblage of many lineages of fishes with somewhat similar morphological organization. When the phylogenetic relationships of these lineages become clearer, the Characidae will no doubt have to be substantially redefined to represent that increased knowledge.

On a lower taxonomic level, we cite as an example a genus that was discussed above. *Astyanax* is a large assemblage of "generalized" characid species all of which are supposed to possess a spectrum of "key" characters that "define" the genus. But it is possible, perhaps likely, that there are several independent evolutionary lineages within *Astyanax*, making it a polyphyletic genus. Many species of *Astyanax* may be more closely related to (are the sister group of) species now placed in other genera. As an example of the latter case, we would cite the genus *Bramocharax* of Central America. Rosen (1972: 12–16) considered the possibility of synonymizing *Bramocharax* with *Astyanax*, but retained the former on the basis of at least one unique character. Nevertheless, it is clear from his discussion that the species now placed in *Bramocharax* have as their sister group one or more species of *Astyanax*. Should these sister group relations be delineated by use of the name *Bramocharax*, then *Astyanax* would have to be considered paraphyletic. To retain a phylogenetic classification, either the *Bramocharax* species would have to be placed within *Astyanax* with their relatives, or the related "*Astyanax*" species would have to be placed in *Bramocharax*.

Stated in another way, if "*Astyanax*" ancestors have given rise to autochthonous specialized lineages (like *Bramocharax*) in various geographical areas of South America, then, to maintain a monophyletic classification, the "*Astyanax*" descendants of those ancestors will have to be placed with their specialized relatives, rather than with their more distant "generalized" relatives.

We expect that the classification of the American characids, and indeed of all the characiforms, will be subject to much reinterpretation and rearrangement as a result of phylogenetic analyses. We would also suggest that the Characiformes is only one of many groups in need of such studies. For example, many members of the gobies (Gobiidae, Eleotridae, and their

Figure 1. Adult live *Paracheirodon simulans*, female above, SL 23.9 mm, male below, SL 21.2 mm, USNM 216973.

putative relatives) and cypriniforms (Cyprinidae and related fishes) display features presumably associated with small size. Both groups are currently the subjects of primarily typological classifications and subjective evolutionary systematic approaches. Understanding of their relationships would be greatly enhanced by phylogenetic analyses.

A HISTORY OF THE NEON TETRA PROBLEM

The neon tetras (Figs. 1–3) are three species of small, brilliantly colored freshwater fishes from South America that have come to the attention of ichthyologists through the aquarium trade. Géry (1960b: 9–13 and 1963: 14) assigned each species to a different genus and referred two of the species to one characid subfamily and the third to another as follows: *Hyphessobrycon simulans* Géry, the green neon, was placed in the Tetragonopterinae (Géry, 1963: 70–71), while *Cheirodon axelrodi* Schultz, the cardinal tetra, and *Paracheirodon innesi* (Myers), the neon tetra, were placed in the Cheirodontinae (Géry, 1960b: 9–13). Although the last two species are well known and kept in aquaria by millions of people because of their intense red and green to blue life colors, all three species remain poorly studied by ichthyologists. In our view former hypotheses concerning their relationships can be rejected both by a reevaluation of evidence provided by former authors and by new evidence presented here. We propose that the three "neon tetras" form a monophyletic group, represented by the genus

Figure 2. Adult live *Paracheirodon axelrodi*, male above, SL 28.9 mm, female below, SL 31.1 mm. Specimens not retained.

Paracheirodon.[1] See the species descriptions for new locality records for these three species and a discussion of their distribution.

Myers (1936: 97) described the first known neon tetra, *Paracheirodon innesi*, and placed it in the genus *Hyphessobrycon*, subfamily Tetragonopterinae, because, among other characters, the holotype appeared to have two rows of premaxillary teeth, the "outer row" represented by a single tooth. Schultz (1956: 42) and Myers and Weitzman (1956: 1) nearly simultaneously described a second species, here called *Paracheirodon axelrodi*, with a color pattern similar to the neon tetra. All these authors recognized that *P. axelrodi* had only one row of premaxillary teeth and that it should be placed in the Cheirodontinae according to the then currently accepted subfamilies. Myers and Weitzman chose to question the validity of at least part of the Cheirodontinae because of the apparent relationship of the two species based on color pattern and body shape. Schultz, on the other hand, chose to place the new fish in

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[1] The type of the genus *Paracheirodon* (Géry, 1960b: 12) is *Hyphessobrycon innesi* Myers (1936) and the name is available for application to all of the neon tetras. Another name, *Lamprocheirodon* Géry (1960b: 13), proposed as a subgenus with *Cheirodon axelrodi* Schultz (1956) as its type, is also available for the three species, but *Paracheirodon* has line precedence over *Lamprocheirodon*.

Figure 3. Adult live *Paracheirodon innesi*, female above, SL 25.1 mm, male below, SL 26.9 mm. Specimens not retained.

Cheirodon, where it "fit" because of its single premaxillary tooth row, thus not upsetting Eigenmann's system.

Géry (1960b: 9–13) examined the relationships of the two neon tetras (then called *Hyphessobrycon innesi* and *Cheirodon axelrodi*) to each other and to other small characids, especially those with one row of premaxillary teeth, grouped as the Cheirodontinae. Géry's analysis is useful, and although to a large extent based on the concepts of generic relationships for the Cheirodontinae published by Eigenmann (1915: 14–17), it includes several hypotheses of possible importance in any study of the phylogeny of small characiforms. Unfortunately, his study was marred by many errors of morphological interpretation (see discussion below on uninformative characters). Géry's work also displays a few interpretive contradictions that in some places made the relationships he proposed unclear.

Because Géry's paper was an attempt to elucidate the "relationships" of many "cheirodontins," including the two neon tetras mentioned above, a review of his basic hypotheses is in order. Géry (1960b: 2–5) proposed to divide the genera of the entire subfamily into two basic groups, the first (divided by Géry at that time into three subgroups) having tricuspid or unicuspid teeth and the second having five or more cusps (*Cheirodon* and seemingly related genera). This was done despite the fact that one species of the second group, *Cheirodon australis* Eigenmann, from Chile, was known to have tricuspid teeth. Subsequently Géry (1973: 81) divided the group with unicuspid or tricuspid teeth into two groups (instead of the three in Géry, 1960b: 2–5), those with mostly unicuspid teeth, the Aphyoditeina, and those having tricuspid teeth, left unnamed. As with the Cheirodontinae itself, we think that these subgroups, as currently proposed, will ultimately be rejected. Géry himself (1960a: 32–34 and b: 1–5, 1973: 81) expressed reservations about the validity of the groups.

Géry (1960b: 5–9) proposed five groups in the genus *Cheirodon*. The first two groups included three or four nominal species, including the type of the genus, *Cheirodon pisciculus* Girard, from the west side of the Andean Cordillera in Peru and Chile. The next two groups are found primarily on the eastern side of the Andes and northward into Central America. Eigenmann (1915: 64) was also aware of this possible division into groups east and west of the Andes, and we concur that this suggested separation is worthy of a detailed investigation, even though, as Géry (1960b: 6) suggested, there appear to be "intermediate" species. Géry's fifth group (1960b: 8) is represented by only *Paracheirodon axelrodi*. Géry (1960b: 9–13) was unsure of the relationships of *P. innesi* but believed that since it did not have teeth with five or more cusps, it could not be a *Cheirodon*.

Of primary interest to us here are those groups proposed by Géry (1960b and 1963) to be related to the neon tetras. Géry (1960b: 8–9) suggested that *P. axelrodi* was "nearer to the type" of *Cheirodon* (*C. pisciculus*) or to *Cheirodon stenodon* Eigenmann than to the small, deep-bodied species occurring mostly east of the Andean Cordillera such as *Cheirodon interruptus* (Jenyns). Géry (1960b: 9) stated that *P. axelrodi* shows similarities to *Myxobrycon* Eigenmann but noted at least one major difference from the latter, poorly known, genus. He then stated that *P. axelrodi* "may be close" to *Pseudocheirodon* Meek and Hildebrand. Fink and Weitzman (1974: 3–5) placed *Pseudocheirodon* as a synonym of *Cheirodon*, noting its close similarity with the groups of *Cheirodon* species east of the Andes. Thus, Géry (1960b: 8–9) proposed that *P. axelrodi* is most closely related to the species west of the Andean mountains but also stated that it is perhaps closely related to a genus and species now placed with the species of *Cheirodon* found to the east of the Andes.

Of the relationships of *Paracheirodon innesi*, Géry (1960b: 9) stated that it ". . . has striking morphological affinities with *Cheirodon* [he does not mention at this point which group of *Cheirodon*, those to the east or those to the west of the Andean mountains], but some structures (in particular the teeth) make it more probably intermediate between the first and second groups of 'tricuspid Cheirodontinae,' being perhaps the link between *Megalamphodus* (for example) and *Cheirodon* (for example)." The genera in Géry's first "tricuspid group" were *Megalamphodus* Eigenmann, *Pristella* Eigenmann, *Pseudopristella* Géry, and *Oligobrycon* Eigenmann. His second "tricuspid group" included *Prodontocharax* Eigenmann and Pearson, *Microschemobrycon* Eigenmann, *Aphyocharacidium* Géry, and *Aphyocheirodon* Eigenmann; it did not include *Cheirodon*, which, as noted above, was grouped with other genera characterized by teeth with five or more cusps. Thus, Géry seemed to say two, contradictory things: first, that *P. innesi* is intermediate between two groups of "cheirodontins" with tricuspid teeth and second, that it is a "link" between *Megalamphodus*, which belongs to one of those groups, and *Cheirodon*, which Géry placed in a group separate from the "tricuspid teeth group."

After apparently disassociating *P. innesi* and *P. axelrodi* in the above manner, Géry (1960b: 13) raised another possibility, stating that although *P. innesi* is "anatomically rather near to *Megalamphodus* or *Oligobrycon* (seeming intermediate between the two already mentioned groups)," it is "also near to a third group represented by the aberrant *Cheirodon axelrodi* (by a remarkable evolutive [sic] convergency or, more probably, by a real phylogenetic affinity)." The evidence Géry used to support his views will be discussed below, but our interpretation of the characters is very different from his.

Géry's understandable indecision and apparent confusion regarding the relationships of the neon tetras may be alluded to by quoting the following statement made by him later (1963: 13) regarding his earlier study (1960b) of these two species. After noting that the two neon tetras, *P. axelrodi* and *P. innesi*, ". . . have unusual skull, jaws and teeth structures," he stated the following: "These peculiarities place them in 'border-groups,' in boundaries between the tetragonopterins on the one hand, and the cheirodontins on the other. Their existence, together with that of several other forms seems even to show that the last named groups are quite artificial and may be united in a natural classification. It was also suggested that, although being technically in different (but very close) genera, both species may have arisen from a common stem. Otherwise their remarkable convergency (same habits and coloration) could not satisfactorily be explained."

Géry (1960b: 1) noted that the above two species had been hybridized by an aquarist. Unfortunately the results of this are unknown to us and apparently have never been published.

In his description of the third neon tetra, *P. simulans*, Géry (1963: 70–71) stated the following: "It is indeed a genuine *Hyphessobrycon* with two well separated rows of teeth on the premaxillary and an elongate pedicel [ascending premaxillary process]." In a footnote, Géry noted that the genus *Hyphessobrycon* perhaps should be split into two genera. Géry did not relate *P. simulans* to any known species of *Hyphessobrycon* and stated that ". . . none seems to be very close to *H. simulans*." Géry (1963: 71) further stated that *P. simulans* has a color pattern similar to that of *P. innesi* and that he believed such a color pattern similarity to be due to convergence. He noted several morphological differences between *P. simulans* and the other two neon tetras in support of this hypothesis.

More recently, Géry suggested yet another possibility regarding the relationship of *P. innesi*. In regard to his studies on the "Aphyoditeina," Géry (1973: 81) noted that the possible relationship of *P. innesi* to the "Aphyoditeina" needs to be considered.

It is difficult to summarize Géry's views about the relationships of the three neon tetras. As noted above, he continued to place them in three different genera, with *Paracheirodon innesi* and *Cheirodon axelrodi* in one subfamily, the Cheirodontinae, and *Hyphessobrycon simulans* in the Tetragonopterinae. He appeared to believe that *P. innesi* and *P. axelrodi* must be related in some way even though possessing "technical" characters that "required" their placement in separate genera and separate sections of the Cheirodontinae. He also stated that these two species belong in "borderline" cheirodontine groups, near the Tetragonopterinae, but suggested (Géry, 1963: 71) that *Hyphessobrycon simulans* acquired its "neon" color pattern independently of *P. innesi* and *P. axelrodi*.

Another hypothesis regarding the relationships of these fishes has been proposed by Scheel and Christensen (1970) and Scheel (1972), who studied the chromosomes of these small characids. They proposed that *P. innesi* and *P. axelrodi* are ". . . distantly related, the similarities [sic] colors reflecting convergence and not close relationships" (Scheel and Christensen, 1970: 31) and that *P. simulans* ". . . is karyotypically much closer to a large number of dissimilar-looking tetras than to the other two neon tetras" (Scheel, 1972:

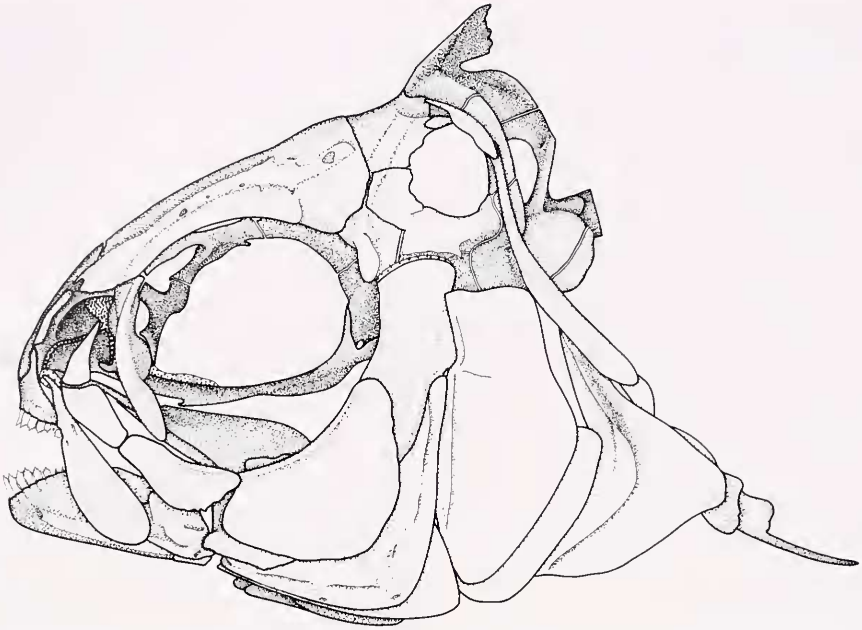

Figure 4. Skull and pectoral girdle of large adult female *Paracheirodon axelrodi*, SL 31.3 mm, USNM 216910, lateral view, left side.

65). These authors' analyses can be faulted for several reasons which are dealt with in more detail below (see discussion on currently uninformative characters). Suffice it to say here that the concept of relationships used appears to be phenetic and there was no attempt by the authors to distinguish derived from primitive similarities in the karyotypes.

In an anonymous introduction to the study of the chromosomes of *P. innesi* and *P. axelrodi* by Scheel and Christensen (1970: 24), the following paraphrased opinion was expressed. To many aquarists the cardinal and neon tetras appear very similar, their most obvious differences being in the extent of the red pigment along the sides of the body. Since the two species also have similar behavior (apparently including breeding behavior) and roughly similar aquarium requirements, a few interested aquarists have concluded that these species are sufficiently alike so that their separate generic placement is of doubtful validity and that they should be placed in one genus. It was then pointed out by the anonymous author that evidence presented by Scheel and Christensen suggested that their similarities are due to convergence. Our own analysis indicates that the aquarists are closer to the truth than most of the various investigators publishing on the subject. One aquarist, Madsen (1975: 162), was so confident of the seemingly obvious relationship between *P. simulans* and *P. axelrodi* that he placed both species in the genus *Cheirodon*. Another author, Van Ramshorst (1981: 142), placed *P. innesi* in *Cheirodon*.

Although we have found synapomorphies that indicate a relationship among the three species of *Paracheirodon* as defined below, we have been unable to formulate a hypothesis of their relationship to any other specific characid group. In

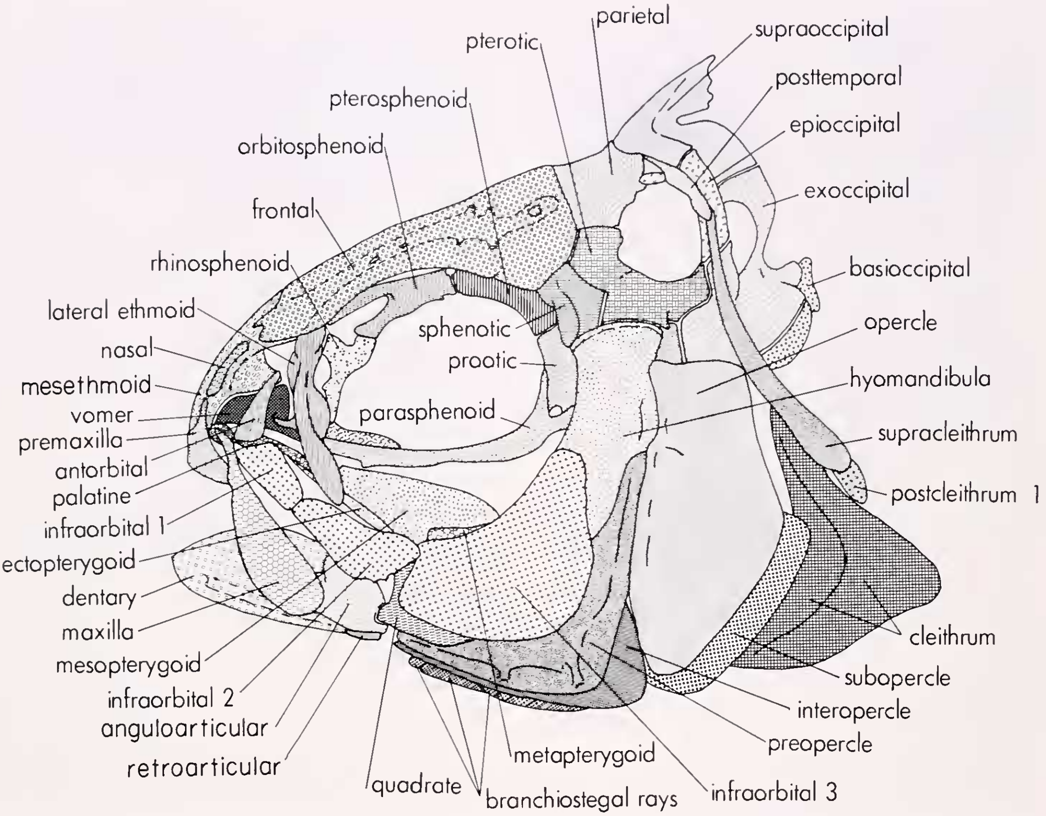

Figure 5. Diagram of skull and pectoral girdle of *Paracheirodon axelrodi* with each bone represented by a different pattern. Adult female, SL 31.3 mm, USNM 216910, lateral view, left side.

part this may be due to the poor morphological information available for possibly related characid groups. Before forming hypotheses of relationship among the various groups of small and miniature characids, those groups need to be diagnosed by further phylogenetic studies. The present contribution is only a beginning attempt to identify monophyletic characid groups.

Paracheirodon Géry

Paracheirodon Géry, 1960b: 12 (type species: *Hyphessobrycon innesi* Myers, by original designation).

Lamprocheirodon Géry, 1960b: 13, as a subgenus (type species: *Cheirodon axelrodi* Schultz, by original designation).

PHYLOGENETIC ANALYSIS OF *PARACHEIRODON*

Below we present evidence for the monophyly of *Paracheirodon*. For each character, the derived state is listed first, followed by the character as found in outgroups.

In the skull figures we use a diagrammatic representation with a standardized pattern for each bone. The skull of *P. axelrodi*, unlabeled in Figure 4, is repeated and labeled in pattern form in Figure 5. These two figures are provided in part as a guide to the use of the remaining skull figures.

The following characters are synapomorphies for the neon tetras.

1) In life there is an intense blue or blue-green lateral body stripe. In other characids, a lateral body stripe is common, most often silvery, or also reddish, red orange, and pale green, but never of the intensity found in *Paracheirodon*.

2) In life dense red pigment is restricted to the region ventral to the lateral stripe. All other American characids in which live pigmentation is known lack the dense pigment of this pattern. Géry (1966a: 116) stated that in freshly preserved *Axelrodia riesei* ". . . the fish is almost entirely of the same red color as that of the cardinal tetra, *Cheirodon axelrodi*; only the belly and lower part of the head are plain; . . ." The distribution of the red pigment of *A. riesei* over most of the body as described by Géry is different from that of *Paracheirodon*. Further, we suspect that the intensity of the color in Géry's specimens of *Axelrodia* can be attributed to fixation artifact caused by formalin. Many small characids with silvery or white abdominal pigment, when fixed in formalin, develop a pink or even red abdominal region. A photograph of *Axelrodia riesei* in life (Géry, 1966a: 111, Fig. 1) shows much less red than the preserved specimen. We know of no other species of American characids whose pigmentation can be compared to that of the *Paracheirodon* species.

The red pigmentation extends well anterior to the pelvic fins in *P. axelrodi* and *P. simulans*. In *P. innesi* the red pigment does not extend to the pelvic-fin base. Lack of a precise outgroup prevents our use of this pigment distribution for phylogenetic evaluation within *Paracheirodon*.

3) A stripe of dark brown or black chromatophores underlies and extends dorsal to the blue lateral stripe. In other characids with a colored lateral stripe the underlying dark chromatophores, when not restricted to the immediate area of the colored stripe, lie ventral to the colored stripe rather than dorsal to it.

4) The pterotic aponeurosis is attached to the cranium near the middle of the anterolateral border of the posttemporal fossa, where it attaches either to the pterotic or sphenotic bones (Figs. 6–8). In other characids examined (Figs. 9–18) this aponeurosis extends from a spinous process of the pterotic bone located at the ventral border of the posttemporal fossa. The pterotic aponeurosis is attached posteriorly to epaxial body musculature in all cases.

5) The joint between the posttemporal and supracleithrum is placed at or dorsal to the midpoint of the vertical length of the posterior border of the posttemporal fossa (Figs. 6–8). In other characids examined (Figs. 9–18) the joint lies at or ventral to the ventral border of the posttemporal fossa.

6) The epioccipital bridge (very reduced and occasionally absent in some specimens of *P. simulans*, Fig. 6) lies at the dorsal border of the posttemporal fossa (Figs. 7, 8). It bisects the fossa in its mid-region or lies just dorsal to it in most characids (Figs. 9–11). In *Hemigrammus erythrozonus* (Fig. 12), *Axelrodia riesei* (Fig. 13), *Brittanichthys axelrodi* (Fig. 14), *Characidium* sp. (Fig. 16), and *Elachocharax geryi* (Fig. 18) the bridge, or parts of it, are placed dorsally but never as far as in the species of *Paracheirodon*. In some characids the epioccipital bridge is absent (Fig. 15 of *Tyttocharax madeirae*, a glandulocaudine, and Fig. 17 of *Klausewitzia aphanes*, a characidiinin). This absence of an epioccipital bridge is most parsimoniously interpreted as independently lost in these two "subfamilies" and in *Paracheirodon simulans*.

7) The ventral posttemporal ligament extends between the ventral arm or process of the posttemporal bone and the intercalar. The latter is located on the lateral surface of that part of the pterotic bone which bears the horizontal semicircular canal. In other characids examined the intercalar and its attached ligament are placed at or very near to the common joint area of the pterotic, exoccipital, and the basioccipital.

8) The dorsal profile of the parietal bone

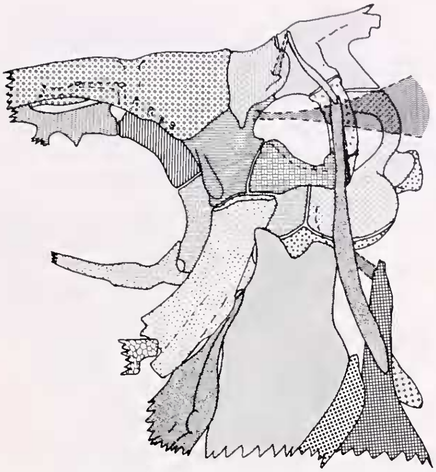

Figure 6. Postocular skull region and dorsal part of pectoral girdle of *Paracheirodon simulans,* adult female, SL 23.9 mm, USNM 216738, lateral view, left side.

Key to Patterns: See Figure 5, p. 351.

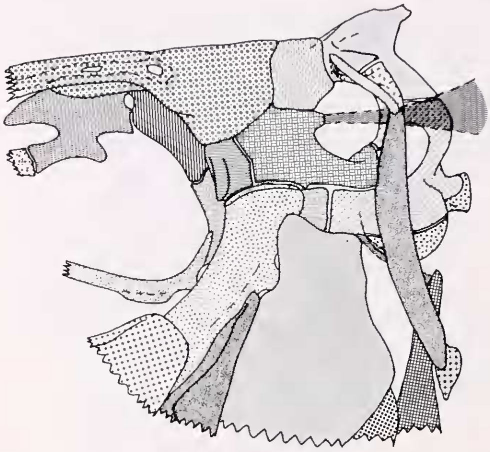

Figure 8. Postocular skull region and dorsal part of pectoral girdle of *Paracheirodon innesi*, adult female, SL 24.6 mm, USNM 216912, lateral view, left side.

Key to Patterns: See Figure 5, p. 351.

is flat or concave in lateral view and the supraoccipital projects dorsally from the posterior border of the parietal (Figs. 6–8). This character is evident in the "pinched nape" look seen in Figures 1 to 3 of live specimens. In other relatively slender characids examined with a relatively elongate body shape, the dorsal profile of the posterior region of the skull is approximately straight (Figs. 9, 11–18). In

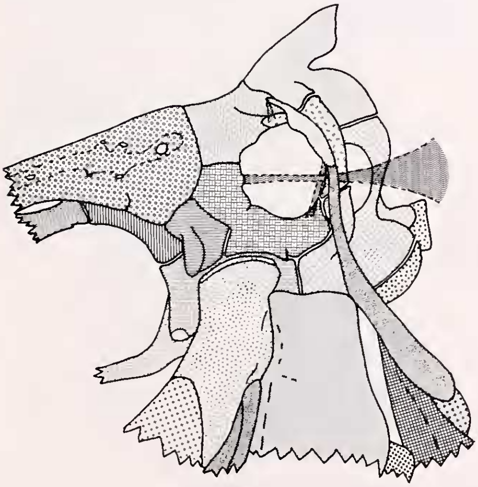

Figure 7. Postocular skull region and dorsal part of pectoral girdle of *Paracheirodon axelrodi,* adult female, SL 31.3 mm, USNM 216910, lateral view, left side.

Key to Patterns: See Figure 5, p. 351.

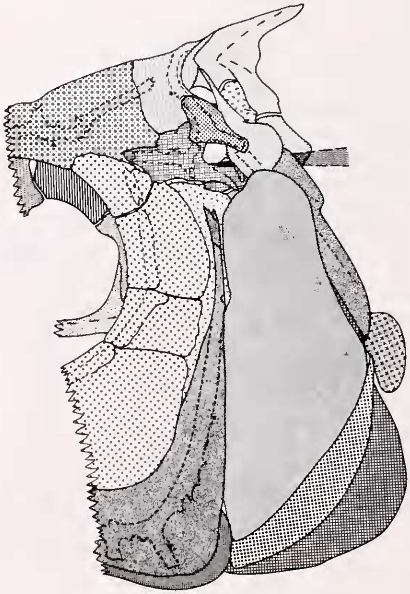

Figure 9. Posterior region of skull and pectoral girdle of *Astyanax fasciatus mexicanus,* female, SL 52.4 mm, MCZ 41365, lateral view, left side.

Key to Patterns: See Figure 5, p. 351.

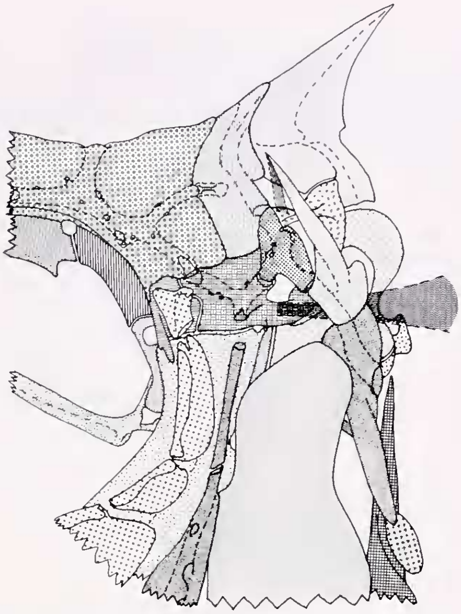

Figure 10. Postocular region of skull and pectoral girdle of *Gymnocorymbus thayeri*, adult, SL 27.5 mm, CAS(IUM) 15881, lateral view, left side.

Key to Patterns: See Figure 5, p. 351.

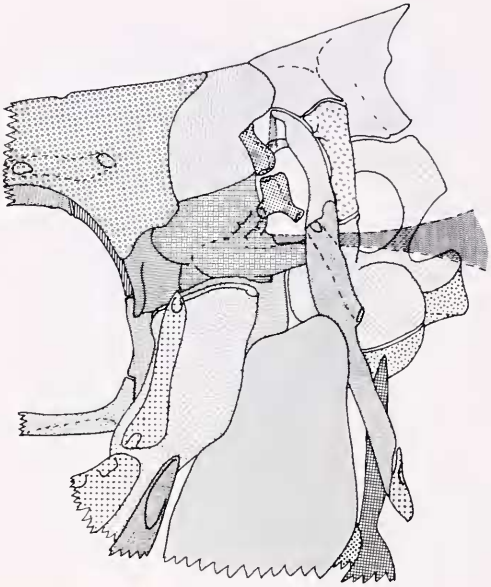

Figure 12. Postocular region of skull and pectoral girdle of *Hemigrammus erythrozonus*, adult male, SL 24.2 mm, USNM 216709, lateral view, left side. Note: Extrascapular of contralateral side is a single bone.

Key to Patterns: See Figure 5, p. 351.

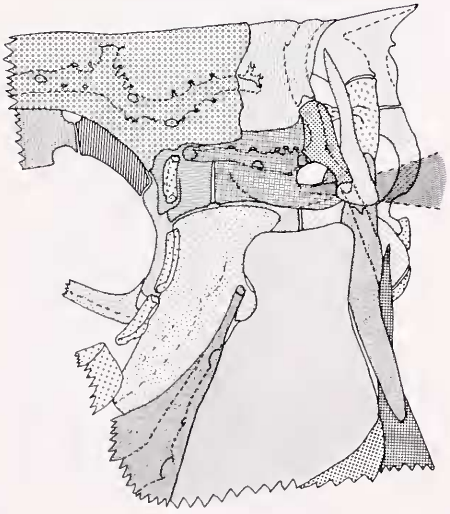

Figure 11. Postocular region of skull and pectoral girdle of *Cheirodon interruptus*, adult female, SL 27.0 mm, FMNH 50629, lateral view, left side.

Key to Patterns: See Figure 5, p. 351.

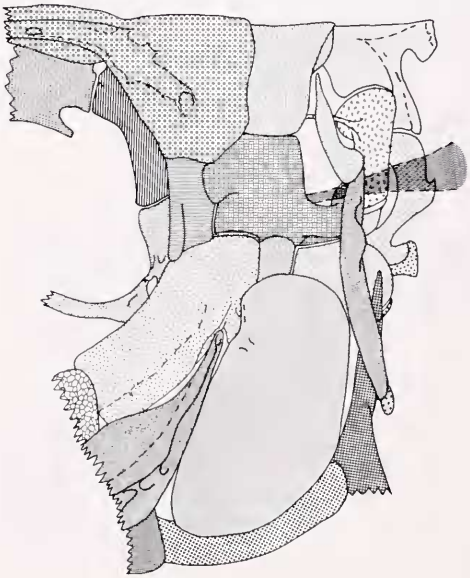

Figure 13. Postocular region of skull and pectoral girdle of *Axelrodia riesei*, SL 16.2 mm, USNM 221681, lateral view, left side.

Key to Patterns: See Figure 5, p. 351.

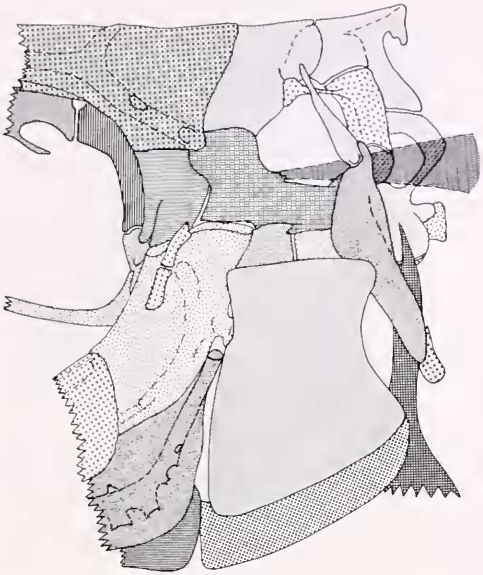

Figure 14. Postocular region of skull and pectoral girdle of *Brittanichthys axelrodi*, adult female, SL 22.2 mm, USNM 221682, lateral view, left side.

Key to Patterns: See Figure 5, p. 351.

deep-bodied characids such as *Gymnocorymbus thayeri* (Fig. 10), the entire dorsal profile from anterior to the epiphyseal bar of the frontal bone and the posterodorsal apex of the supraoccipital spine is concave, with the parietal and supraoccipital curving dorsally.

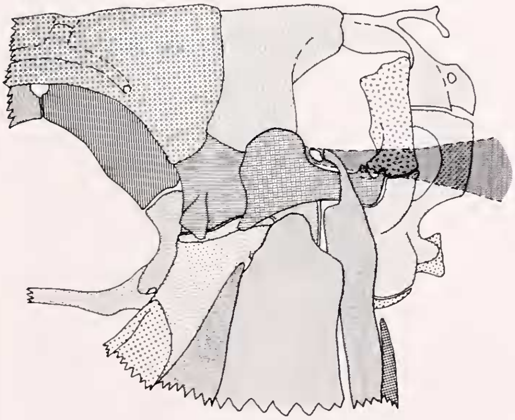

Figure 15. Postocular region of skull and pectoral girdle of *Tyttocharax madeirae*, adult male, SL 17.9 mm, USNM 222007, lateral view, left side.

Key to Patterns: See Figure 5, p. 351.

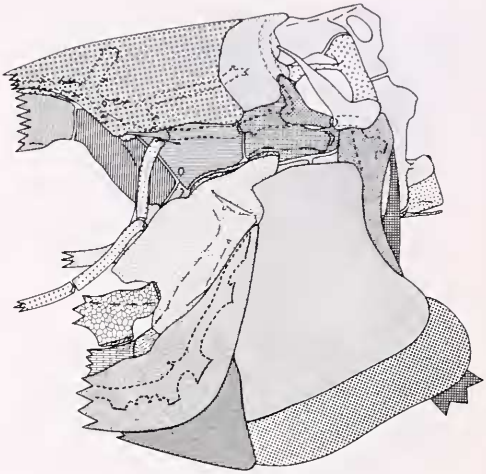

Figure 16. Postocular region of skull and pectoral girdle of *Characidium* sp., adult, SL 35.0 mm, USNM 222017, lateral view, left side.

Key to Patterns: See Figure 5, p. 351.

KEY TO SPECIES OF *PARACHEIRODON*

1a. Premaxilla with teeth in 2 distinct rows (Fig. 19A–E); outer row of 1 or sometimes 2 conical teeth; inner row of 4–5 multicuspid teeth with 5–9 cusps; maxilla usually toothless, sometimes with 1 conical tooth; dorsal fin with 7–8, usually 8, branched rays; pectoral fin with 7–9, usually 8, branched rays; pelvic fin with 5–6, usually 6, branched rays; blue-green stripe on body sides of live specimens posteriorly terminating at caudal-fin base .... *Paracheirodon simulans*

1b. Premaxilla with teeth in 1 row or with 1 row having 1 or 2 teeth somewhat offset anteriorly at their bases (Fig. 20A–D, Fig. 21A–E, Fig. 22A–C) [sometimes aged aquarium specimens will have abnormal teeth in two irregular rows (Fig. 23A–D)]; premaxillary tooth row with 5 teeth, each with 5 cusps (specimens less than 10 mm SL with 3 cusps) or with 6–7 teeth, each with 3 cusps; maxilla with 1 tooth having 3–5 cusps or 2–3 teeth having 3 cusps; dorsal fin with 8–9, almost always 9, branched rays; pectoral fin with 10–13, usually 10–12, branched rays; pelvic fin with 7, rarely 6, branched rays; blue-green stripe on body sides of live specimens pos-

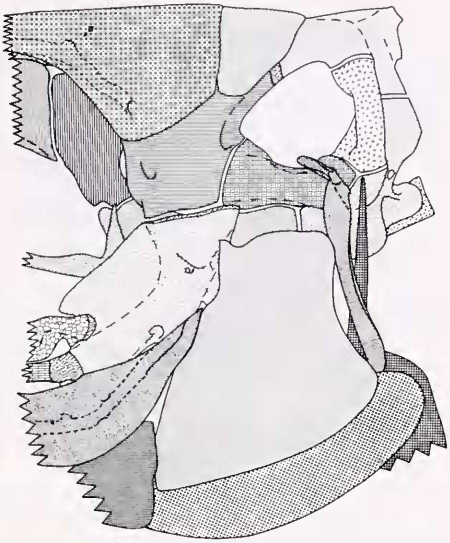

Figure 17. Postocular region of skull and pectoral girdle of *Klausewitzia aphanes*, adult, SL 14.9 mm, USNM 221995, lateral view, left side.

Key to Patterns: See Figure 5, p. 351.

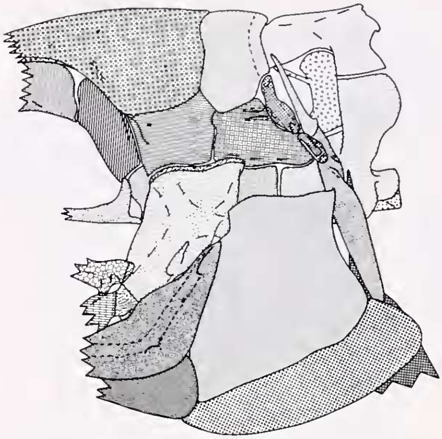

Figure 18. Postocular region of skull and pectoral girdle of *Elachocharax geryi*, small adult, SL 12.5 mm, USNM 215288, lateral view, left side.

Key to Patterns: See Figure 5, p. 351.

teriorly terminating near adipose-fin base, not reaching caudal-fin base 2

2a. Premaxilla with 1 row of 5 teeth each having 5 cusps (3 cusps in specimens of less than 10 mm SL) (Fig. 20A–D); maxilla with 1 tooth with 5 cusps; dentary with anterior teeth often having 5, but up to 7 cusps; ventral-limb gill rakers 12–14, usually 12–13; perforated lateral-line scales 5–8, usually 6–7; red pigment on body sides of live specimens extending well anterior to pelvic-fin base .... *Paracheirodon axelrodi*

2b. Premaxilla with 1 row of 6–7, rarely 8, teeth each having no more than 3 cusps (Fig. 21A–E, Fig. 22A–C); often 1 or sometimes 2 of these teeth offset anteriorly at their bases giving appearance of 2 rows unless flesh is cleared to base of teeth where their approximation to 1 row can be seen (Fig. 21A,B); maxilla with 2–3 teeth, each with no more than 3 cusps (Fig. 21C,D); each dentary tooth with no more than 3 cusps (Fig. 21F); ventral-limb gill rakers 10–11, usually 11; perforated lateral-line scales 3–6, usually 4–5; red pigment on body sides of live specimens not extending anterior to pelvic-fin base .... *Paracheirodon innesi*

Paracheirodon simulans (Géry)
Figures 1, 6, 19C, 24C, 25; Tables 1, 4 to 7

Hyphessobrycon simulans Géry, 1963: 15, original description, Brazil, "in the Rio Purus" (see discussion, Appendix 2).—Géry, 1966c: 231, correction of type locality.—Scheel, 1972: 60, relationships based on chromosomes.—Géry, 1977: 474, 563, 587, relationships.

Cheirodon simulans (Géry), Madsen, 1975: 162, aquarium description, referral of *P. simulans* to *Cheirodon*.

Specimens Examined. 1, paratype, USNM 197510, SL 16.1 mm, Brazil, Amazonas, Rio Jufari (=Tupari) 1°15′S, 62°0′W), tributary to Rio Negro near mouth of Rio Branco, November 1962, H. W. Schwartz [Note: original type locality listed by Géry (1963) as "lower Rio Purus," Amazonas, Brazil was corrected to that given above by Géry (1966c)].—12, USNM 216896, SL 12.0–13.3 mm, Venezuela, Amazonas, caño tributary to Río Orinoco approximately 14 km east of San Fernando de Atabapo (4°4′N, 67°42′W), 14 April 1972, Alvaro Cortez.—Following lots with same locality information as USNM 216896 preceeding: 11, MBUCV-V 7283, SL 10.4–14.2 mm; 12, ANSP 138020, SL 10.3–13.7 mm; 3 alizarin preparations, USNM 216915, SL 12.5–14.6 mm.—1, MBUCV-V 7471, SL 17.8 mm, Venezuela, Amazonas, caño 20 km east of San Fernando de Atabapo (4°4′N, 67°42′W) towards Santa Bárbara, 13 April 1972, Alvaro Cortez.—3, USNM 216750, SL 13.1–15.0 mm and 3,

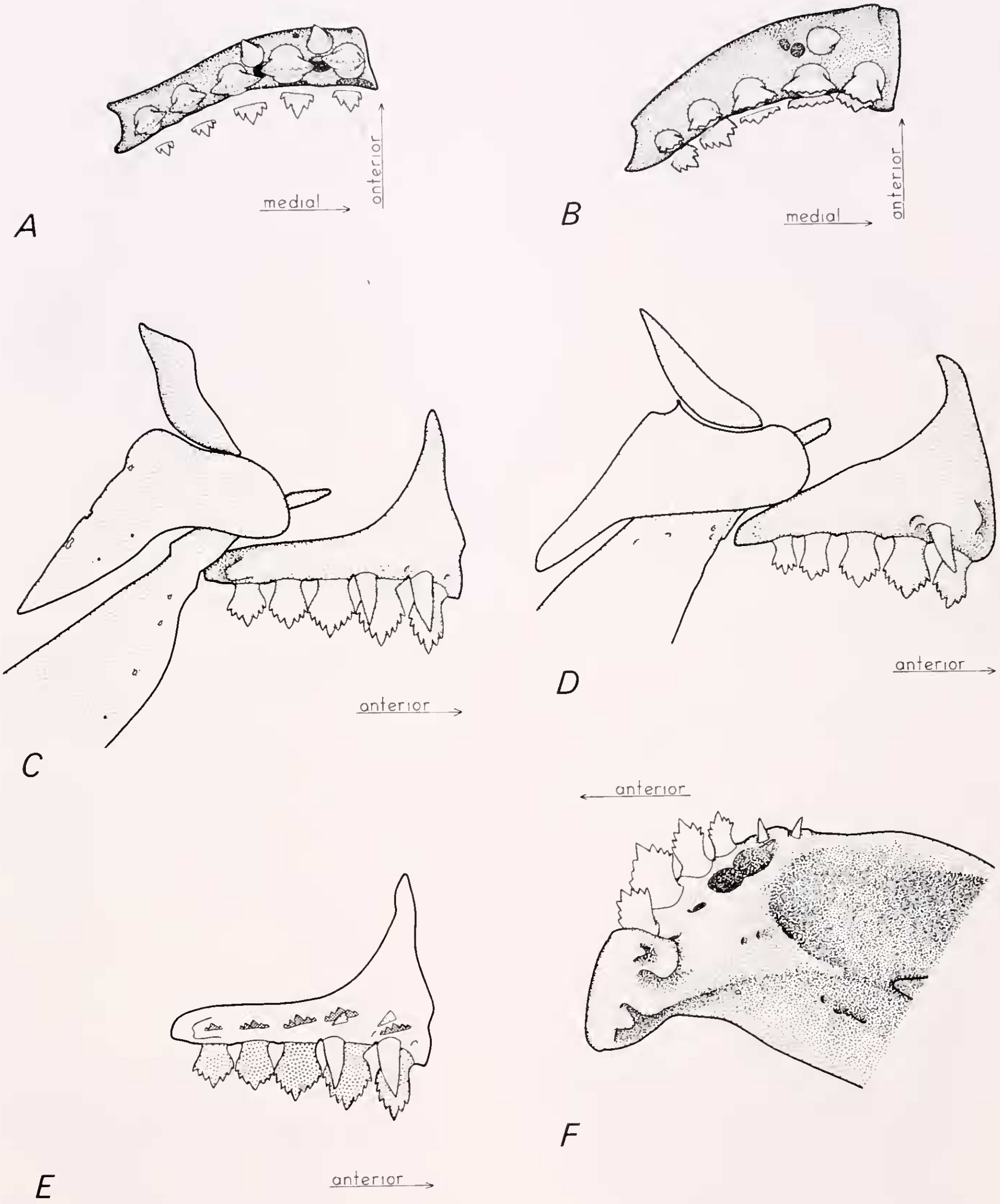

Figure 19. Teeth and jaws of *Paracheirodon simulans*. A. Premaxilla, ventral view, right side of adult SL 20.0 mm, USNM 216913. B. Premaxilla, ventral view, right side of large adult, SL 23.9 mm, USNM 216913. C. Premaxilla, maxilla, infraorbital 1, antorbital, and reduced nasal bone, anterolateral view, right side of adult, SL 20.0 mm, USNM 216913. D. Same series of bones as in C. preceeding (nasal bone absent), anterolateral view, large adult, SL 23.9 mm, USNM 216913. E. Transparency of premaxilla, anterolateral view of adult, SL 20.0 mm, USNM 216913, showing position of replacement teeth within bone. F. Dentary, medial view, right side of large adult, SL 23.9 mm, USNM 216913.

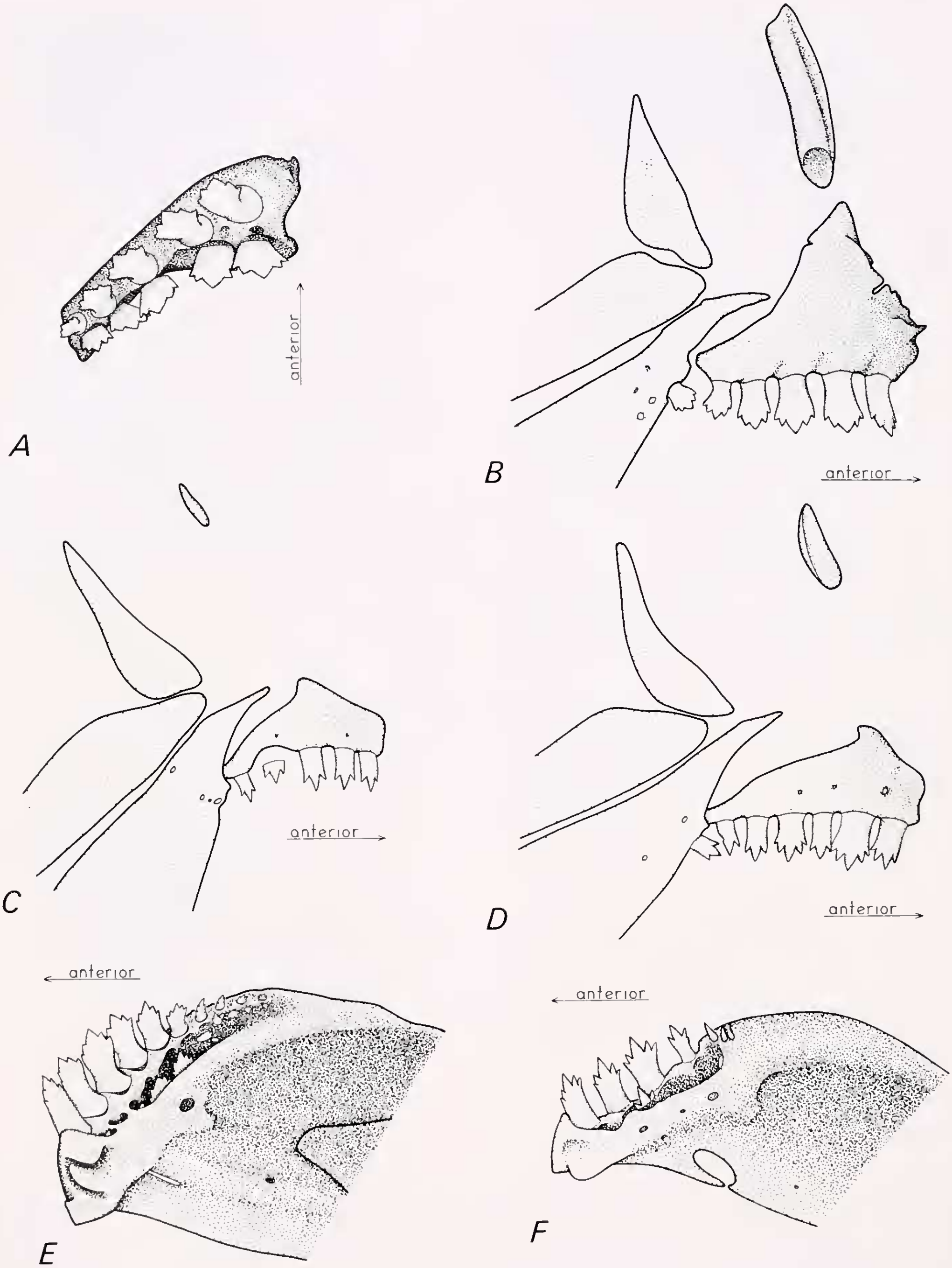

Figure 20. Teeth and jaws of *Paracheirodon axelrodi*. A. Premaxilla, ventral view, right side of large adult, SL 33.1 mm, USNM 216910. Nearly fully developed replacement teeth posterior to teeth ankylosed to jaw produce appearance of two tooth rows. B. Premaxilla, maxilla, infraorbital 1, antorbital, and nasal bones in anterolateral view, right side of large adult, SL 33.1 mm, USNM 216910. C. Same series of bones as in B. preceeding, anterolateral view, right side of juvenile, SL 10.1 mm, MCZ 52459. D. Same series of bones as in B. preceeding, anterolateral view, right side of juvenile, SL 11.9 mm, MCZ 52459. E. Dentary, medial view, right side of large adult, SL 33.1 mm, USNM 216910. F. Dentary, medial view, right side of juvenile, SL 10.1 mm, MCZ 52459.

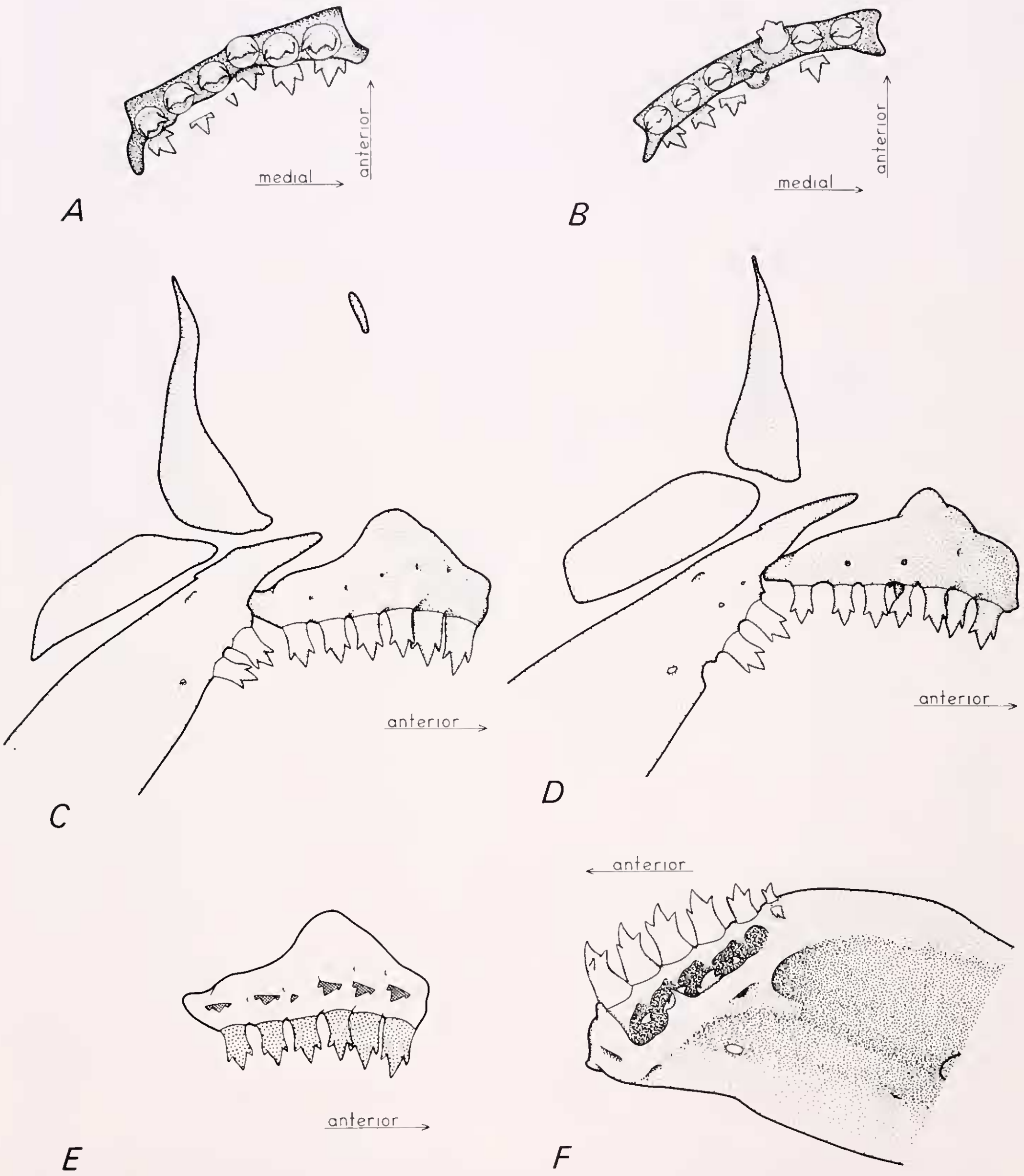

Figure 21. Teeth and jaws of *Paracheirodon innesi*. A. Premaxilla, ventral view, right side of adult, SL 21.5 mm, USNM 216912. B. Premaxilla, ventral view, right side of adult, SL 21.8 mm, USNM 216912. C. Premaxilla, maxilla, infraorbital 1, antorbital, and nasal of adult, anterolateral view, right side, adult, SL 21.5 mm, USNM 216912. D. Same series of bones as in C. preceeding, anterolateral side of adult, SL 21.8 mm, USNM 216912. E. Transparency of premaxilla, anterolateral view of adult, SL 21.5 mm, USNM 216912, showing position of replacement teeth within bone. F. Dentary, medial view, right side of adult, SL 21.5 mm, USNM 216912.

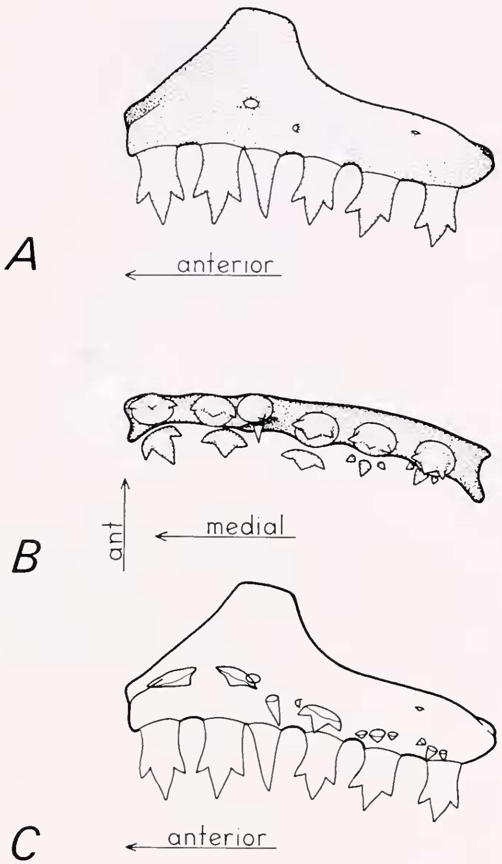

Figure 22. Premaxillary bone of *Paracheirodon innesi* juvenile, SL 13.5 mm, MCZ 52156. A. Anterior view, left side. B. Ventral view, left side. C. Anterior view, left side; bone shown as transparent so that position of replacement teeth may be seen.

MBUCV-V 8653, Venezuela, Amazonas, upper Rio Orinoco, affluent of Caño Cadabaudi at Esmeralda (3°11′N, 65°34′W), 25 January 1969, Francisco Mago-Leccia, Jose Mosco, Antonio Machado.—Following specimens all collected for aquarium trade, some with at least modestly helpful locality information: 13, USNM 216737, SL 10.1–19.6 mm, Colombia, Vichada, collected "out of Puerto Correño" (6°12′N, 67°30′W) at mouth of Río Meta into Río Orinoco, July–September 1975 for Capt. E. Siaz. Note: it is very likely that these fishes were collected at various sites south of Puerto Correño, in tributaries of the Río Orinoco in both Colombia and Venezuela.—Following lots have same locality information as USNM 216737 immediately preceeding: 12 alizarin preparations, USNM 216736, SL 9.3–20.3 mm; 7, USNM 216911, SL 11.2–13.5 mm; 10 alizarin preparations, MCZ 52339, SL 10.9–19.5 mm; 4, ANSP 137964, SL 11.5–16.6 mm; 2, BMNH 1977.3.11.5–6, SL 11.9–17.3 mm; 4, MZUSP, SL 10.4–19.1 mm.—5, USNM 216738, SL 17.0–23.5 mm and 4 alizarin preparations, USNM 216913, SL 21.2–23.9 mm, aquarium specimens possibly from same locality as USNM 216737 or from some aquarium collection station on upper Rio Negro in Amazonas, Brazil, 1974 or 1975.

Paracheirodon simulans occurs in the upper Rio Negro region of Brazil from near the mouth of the Rio Branco and in the Río Orinoco in the region of San Fernando de Atabapo and the mouth of Río Meta into the Río Orinoco. The original collector, Hans Willi Schwartz, told us that *P. simulans* also occurs in the upper Rio Negro areas between the mouth of the Rio Branco and the Río Orinoco headwaters and that although the ranges of *P. axelrodi* and *P. simulans* occur in the same general geographical areas, they in fact do not live in the same portions of the tributaries of large rivers such as the Rio Negro and Río Orinoco. He found *P. simulans* in the upper sections of these tributaries away from the main river and *P. axelrodi* in the lower portions, in the *varzea* and *terra firme* areas. Both species live in *terra firme* streams but apparently not in the same localities.

Description. See Table 1 for morphometrics and meristics of individual population samples. Morphometrics given below are totals for all samples, including some not recorded in Table 1. Specimens from Venezuela were not measured and scales could not be counted because they were partly deossified and very soft, having been in unbuffered formalin for several years. Specimens measured from vicinity of Puerto Correño are aquarium imports, most of which were preserved a few weeks after reaching the United States. We offer these measurements only as the best available for this species and point out that aquarium and transportation conditions may have altered the growth of these specimens.

Body moderately elongate, not compressed, greatest depth at a vertical line near origin of pelvic fins. Predorsal body profile moderately convex to nape where it is concave. Dorsal profile of head slightly convex. Body profile very slightly or not at all elevated at dorsal-fin origin; slightly convex or straight along dorsal-fin base; straight to slightly convex between dorsal-fin base and adipose-fin origin.

Table 1. Morphometrics and meristics of *Paracheirodon simulans*.†

		Colombia, Puerto Correño				
			Range			
	Paratype	n	Low	High	$\bar{X}$	SD
Standard length	15.4	25	9.6	20.2	15.7	
Greatest body depth	29.9	25	25.0	31.3	28.1	1.525
Snout to dorsal-fin origin	56.5	24	51.2	55.2	53.5	1.226
Snout to pectoral-fin origin	27.9	25	23.8	30.2	27.2	1.395
Snout to pelvic-fin origin	51.3	24	46.8	51.8	49.5	1.105
Snout to anal-fin origin	65.6	25	58.6	66.3	63.3	1.792
Eye to dorsal-fin origin	41.6	24	35.7	42.1	38.2	1.482
Dorsal-fin origin to caudal-fin base	49.4	24	45.5	52.1	49.9	1.561
Caudal peduncle depth	11.7	25	8.3	11.0	10.1	0.699
Caudal peduncle length	15.6	25	14.2	17.9	16.2	0.757
Pectoral-fin length	16.9	25	16.0	19.8	18.2	1.020
Pelvic-fin length	12.3	23	12.7	16.3	14.7	0.890
Dorsal-fin base length	12.3	24	10.2	12.9	11.4	0.676
Longest dorsal-fin ray length	25.3	22	21.9	26.9	24.2	1.293
Anal-fin base length	23.4	25	22.0	26.3	23.6	1.108
Longest anal-fin ray length	18.8	22	16.7	21.7	19.6	1.279
Bony head length	26.0	25	21.9	28.1	24.9	1.248
Horizontal eye diameter	42.5	25	39.6	51.4	44.2	3.068
Snout length	22.5	25	16.1	23.8	19.7	1.914
Least bony interorbital width	32.5	23	29.6	36.4	32.6	1.972
Upper jaw length	35.0	25	32.4	43.8	35.9	2.741
Branched dorsal-fin rays	8	31	7	8	7.7	0.445
Branched pectoral-fin rays	8	32	7	9	8.1	0.354
Branched pelvic-fin rays	6	32	5	6	6.0	0.177
Branched anal-fin rays	15	32	14	18	16.0	0.822
Horizontal scale rows between dorsal fin and pelvic fin	9	22	9	9	9.0	0.000
Predorsal scales	10	22	10	10	10.0	0.000
Perforated lateral-line scales	—	20	0	5	2.6	1.569
Lateral series scales	32	21	29	32	30.9	0.700
Horizontal scale rows around caudal peduncle	12	22	12	12	12	0.000
Dorsal-limb gill rakers	6	42	5	6	5.9	0.328
Ventral-limb gill rakers	11	42	10	12	11.2	0.484
Vertebrae	32	42	32	33	32.4	0.507

† Paratype USNM 197510 and from Puerto Correño, Colombia, USNM 216737, USNM 21091, and MCZ 52339. Standard length is expressed in mm. The next 16 measurements (through head length) are percentages of standard length. The following four measurements are percentages of bony head length.

Caudal peduncle slightly concave in both dorsal and ventral profiles. Dorsal fin midway between caudal-fin base and snout tip or slightly nearer caudal-fin base. Ventral body profile slightly convex from anterior tip of lower jaw to posterior anal-fin termination.

Head and snout relatively short, snout blunt. Mouth terminal. Gape angled somewhat anterodorsally from mandibular joint to snout tip. When mouth closed, maxilla extends posteriorly to a point approximately on a vertical line drawn ventrally from anterior border of pupil.

Dorsal-fin rays ii-7 to ii-8, usually ii-8 (rarely iii-8 with first unbranched ray extremely short), n = 34; adipose fin present in all specimens; anal-fin rays iii-15 to iii-

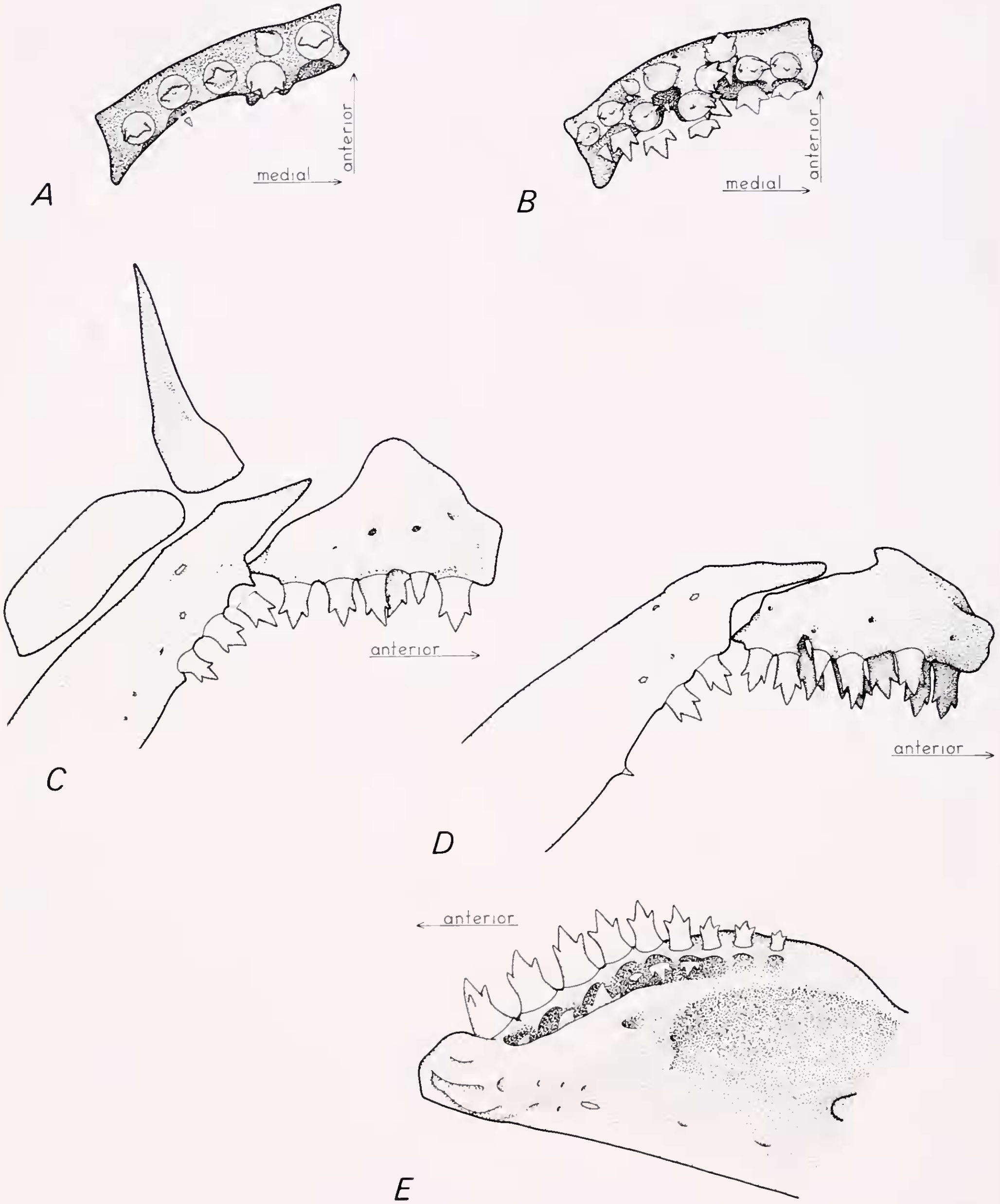

Figure 23. Teeth and jaws of *Paracheirodon innesi*. A. Premaxilla, ventral view of 4 year adult, SL 25.7 mm, USNM 216912. B. Premaxilla, ventral view of 4 year adult, SL 24.6 mm, USNM 216912. C. Premaxilla, maxilla, infraorbital 1, and antorbital (nasal is absent), anterolateral view, right side of adult, SL 25.7 mm, USNM 216912. D. Premaxilla and maxilla, anterolateral view, right side of adult, SL 24.6 mm, USNM 216912. E. Dentary, medial view, right side of adult, SL 25.4 mm, USNM 216912.

18, usually iii-16 (once iv-16 and twice iv-17), n = 34; pectoral-fin rays i-7 to i-9, usually i-8, n = 34; pelvic-fin rays i-5 to i-6, (only one specimen with i-5), n = 34; caudal-fin rays 10/9, n = 34. No bony pelvic-fin hooks found in mature male specimens.

Scales cycloid. Lateral line incomplete (or absent, one specimen), perforated lateral-line scales 0 to 5, usually 3, n = 24; scales in a lateral series 29 to 33, usually 31, n = 25; scale rows between anterior dorsal-fin base and pelvic-fin base 9, n = 28; predorsal scales 9 to 10, usually 10 (9 in one specimen), n = 28; horizontal scales rows around caudal peduncle 12, n = 28.

Dorsal-limb gill rakers 5 to 7, usually 6, n = 42; ventral-limb gill rakers 10 to 12, usually 11, n = 42.

Total number of vertebrae including Weberian apparatus and terminal compound centrum 32 to 34, usually 32, n = 32.

Dental Morphology. Premaxilla with two tooth rows, an inner row of four to five multicuspid teeth and an outer row of one to two conical teeth (Fig. 19A–E). Smallest specimens available to us, SL 11.1 and 11.4 mm, all USNM 216911, with four inner row premaxillary teeth; available specimens larger than preceding all with five. Tooth-cusp formula variable in the wild-caught specimens; representative cusp numbers 6653 [6 (median tooth), 6 (tooth lateral to median tooth), 5 (next lateral in series), 3 (lateral tooth)] (in a specimen 11.4 mm SL), 67763 (SL 11.8 mm), and 69865 (SL 13.8 mm), USNM 216911. Note that in larger specimens two teeth immediately lateral to symphyseal tooth have greatest number of cusps. Positive correlation occurs between fish size and total number of cusps on inner-row teeth, based on our small sample of wild-caught specimens (USNM 216911), SL 11.1 to 13.8 mm, n = 7, $\bar{X} = 12.2$. In these specimens, total cusp number (added over all inner row teeth) gave regression statistics of: y-intercept = 26.0; slope = 4.3; correlation coefficient = 0.87. The few adult specimens available are aquarium raised and are not analyzed statistically; nevertheless, we report SL and tooth formula here for comparison with wild-caught juveniles: SL 20.2 mm, 79977; SL 21.1 mm, 57655; SL 23.9 mm, 68755; all USNM 216736. The degree of variability of these three specimens may be the result of their artificial diet. Nevertheless, the "adult" tooth configuration may be reached at about SL 13 to 14 mm. A more precise statement is not possible since we have no wild-caught adults. We cannot describe the "adult" configuration with certainty but only estimate it from the samples at hand.

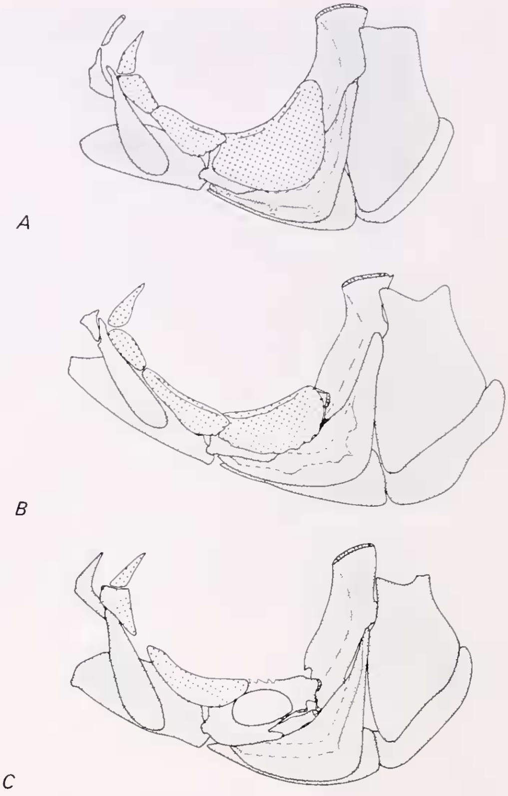

Figure 24. Face bones of the neon tetras. Circumorbital bones represented by plus-sign (+) pattern. Lateral view, left side. A. *Paracheirodon axelrodi*, SL 31.3 mm, USNM 216910. B. *Paracheirodon innesi*, SL 16.4 mm, MCZ 52156. C. *Paracheirodon simulans*, SL 20.4 mm, USNM 216738.

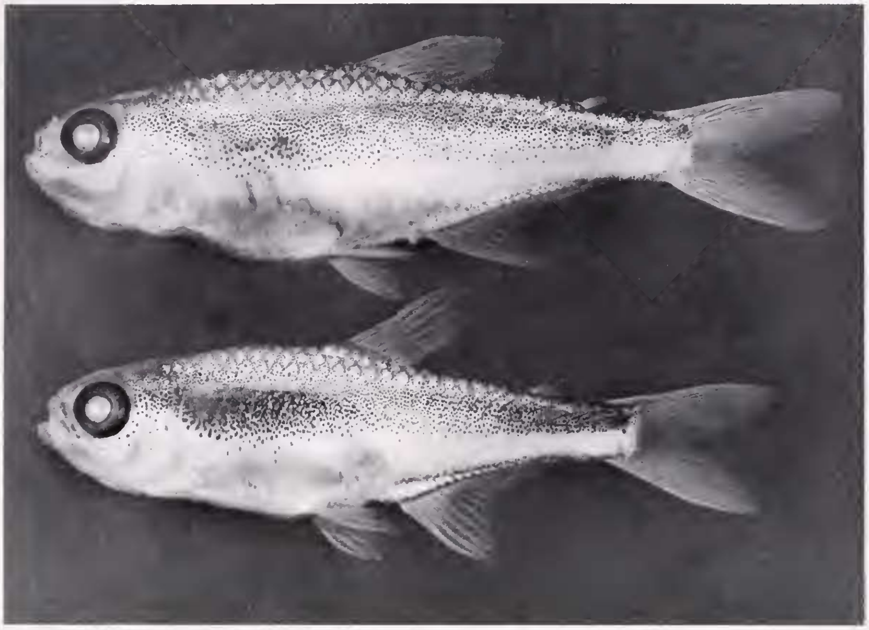

Figure 25. *Paracheirodon simulans*, collected from near Puerto Correño, Colombia, either in Venezuela or Colombia, USNM 216973, female above, SL 20.1 mm, male below, SL 17.6 mm.

There is usually a single, conical, outer row premaxillary tooth but occasionally a second tooth also is present. Again, our limited sample prevents a definitive statement about tooth numbers, but the number of outer row teeth apparently is not correlated with body size longer than about 11 mm SL since two teeth are present in specimens SL 11.5 and 13.5 mm (USNM 216911) and a single tooth is present in other wild-caught specimens. Tooth replacement patterns confirm that the outer tooth row in *P. simulans* is a "true" second row. In Figure 19A replacement trenches (see Roberts, 1967) are clearly visible posterior to the two outer row teeth and small replacement teeth are present in the trenches. Figure 19E is a diagrammatic representation from the anterior aspect of the same premaxilla illustrated in Figure 19A; in it the conical outer row replacement teeth are visible dorsal to the functional conical teeth. Note in both figures that the developing multicuspid replacement teeth (embedded in fleshy tissue) for the inner tooth row lie posterodorsal to the functional teeth. Maxillary teeth are not present in examined specimens, with the exception of one conical tooth on one side of a single specimen (14.4 mm SL) from USNM 216915.

A single row of six to nine teeth is present on the dentary, the medial four teeth being larger (Fig. 19F). Specimens from USNM 216911, discussed above, have the following tooth formula (from the symphysis laterally): (tooth 1) seven to nine, usually seven cusps; (tooth 2) six to seven, usually seven cusps; (tooth 3) five to seven cusps, usually seven cusps; (tooth 4) three to seven, usually three or five cusps; (tooth 5) one to three, usually one cusp; remainder conical. In our small sample of juvenile fish we found no apparent correlation between the cusp number and the SL.

Color Pattern. In life, *P. simulans* (Fig.

1) back olive brown with reticulate dark chromatophore pattern as described for color in alcohol, below. Intense iridescent blue-green lateral stripe extends from skin over infraorbital bones, over cornea of eye (evenly distributed over cornea), over cheeks and opercle, along sides of body, and ends at caudal-fin base. Blue lateral stripe broadest at vertical from pelvic-fin insertion or from just anterior to pelvic-fin insertion. Dense stripe of black chromatophores visible dorsal to blue-green stripe, broadest in region between opercle and posterior termination of dorsal-fin base. Poorly defined stripe of scattered dark chromatophores present ventral to blue lateral stripe. Numerous erythrophores scattered along myosepta between lateral blue stripe and anal-fin base, and scattered anteriorly as far as a point midway between opercle and pelvic-fin base in some specimens. In most specimens, erythrophores extend only slightly anterior to a vertical from pelvic-fin insertion. When erythrophores expanded, entire area between lateral blue stripe and anal-fin base red; when erythrophores contracted, area between blue stripe and anal-fin base light reddish brown. Belly silvery white, reflecting light blue ventrally under some light conditions. Fins hyaline except for very pale white area in some specimens along anterior three fin rays of dorsal fin; in anterior region of anal fin, extending to posterior border of anterior branched fin ray; and in center of adipose fin.

Compared to *P. innesi* and *P. axelrodi*, *P. simulans* with more green in lateral stripe and red sides less brilliant (sometimes virtually lacking in disturbed individuals). Iridescent green covers more of head, i.e., more of eye, infraorbitals, cheeks, and opercle. Blue-green lateral stripe broader in proportion to that of those species.

In alcohol, *P. simulans* (Fig. 25) with ground color light cream brown. Scale pocket margins of dorsum and two to three ventrally successive lateral scale rows lined with dark brown chromatophores, giving a reticulate pattern. Small brown chromatophores may be scattered within scale pocket areas defined by marginal dark chromatophores. Midlateral stripe extends from just posterior to eye to dorsal half of caudal-fin base. Large dark chromatophores on infraorbital 1 probably an anterior extension of lateral stripe. Dorsal border of lateral stripe lies about two and a half scale rows ventral to dorsal-fin origin; maximum width of lateral stripe about three scales. Belly sometimes with a few scattered dark chromatophores. Peritoneum with numerous dark chromatophores, more obvious in smaller specimens. Numerous small dark chromatophores over tips of jaws and dorsum of head, these extending as thin line to caudal-fin base, marking dorsal midline. Dark chromatophores sparsely distributed over infraorbitals and opercle. Numerous small dark chromatophores present along ventral border of orbit. Small dark chromatophores lie along anal-fin base and along line marking conjunction of anal-fin musculature and hypaxial body musculature; these lines converge at posterior termination of anal-fin base and continue as a well-defined dark line along ventral edge of caudal peduncle. Small dark chromatophores line fin-ray borders of all fins; interradial membranes without dark chromatophores. Adipose fin without chromatophores or with very few small dark chromatophores.

Paracheirodon axelrodi (Schultz)
Figures 2, 4, 5, 7, 20, 24A, 26;
Tables 2, 4 to 7

Cheirodon axelrodi Schultz, 1956: 42, original description, Brazil "somewhere near Porto Velho, Amazonas" (see discussion, Appendix 2).—Axelrod, 1956: 16, type locality.—International Commission of Zoological Nomenclature 1957: 87, priority of *Cheirodon axelrodi* in favor of *Hyphessobrycon cardinalis*.—Géry, 1960b: 8, relationships.—Géry, 1963: 71, relationships.—Post, 1965: 47, chromosome numbers.—Scheel and Christensen, 1970: 24, relationships based on chromosomes.—Scheel, 1972: 60, relationships based on chromosomes.—Géry, 1977: 546, 563, relationships.—Kullander, 1978: 274, comments on distribution.

Hyphessobrycon cardinalis Myers and Weitzman, 1956: 1, original description, Brazil, "Rio Negro, Amazonas" (see discussion, Appendix 2).—Meinken, 1956: 89, type locality.—Ladiges, 1956: 116, discovery.—Hoedeman, 1956: 154, type locality, name priority and relationships.—Weitzman, 1956: 257, type locality.

Specimens Examined. Holotype, USNM 164483, SL 22.4 mm; 1, paratype, USNM 164484, SL 20.0 mm, Brazil, Amazonas, stream near Tomar (=Thomar) (0°25′S, 63°55′W), Rio Negro, 1956, collected for Paramount Aquarium Inc. [Note: original locality listed by Schultz (1956) as "near Porto Velho, Brazil," (State of Rondonia, Brazil) discussed in Appendix 2.] Holotype, *Hyphessobrycon cardinalis* (=*P. axelrodi*), CAS(SU) 48710, SL 22.5 mm, 8 paratypes, CAS(SU) 48711, and 2 alizarin preparations CAS(SU) 48712, SL 19.5–21.5 mm, Brazil, Amazonas, Rio Negro near Tomar (0°25′S, 63°55′W), "winter of 1955–1956," for Paramount Aquarium Inc. [Note: original type locality given as "Rio Negro, Amazonas, Brazil;" more precise locality data above originally withheld from publication at request of Paramount Aquarium Inc.].—10, USNM 216901, SL 10.5–24.5 mm, Brazil, Amazonas, Rio Negro, an igarapé of varzea at Tapurucuara (1°30′N, 65°2′W), 19 October 1972, Paulo Vanzolini for EPA.—Following lots with same locality data as USNM 216901 immediately preceding: 15, MZUSP; 5, ANSP 138018, SL 12.3–24.1 mm.—6, USNM 216900, SL 14.7–24.4 mm, Brazil, Amazonas, Rio Negro, São João near Tapurucuara (1°30′N, 65°2′W), 24 October 1972, Paulo Vanzolini for EPA.—Following lots with same locality data as USNM 216900 preceding: 6, MCZ 52460, SL 11.4–22.3 mm; 13, MZUSP; 5, MZUSP; 5, USNM 216905, SL 22.5–25.0 mm; 30, MZUSP; 10, USNM 216902, SL 12.0–22.8 mm; 8, MCZ 52461, SL 11.5–20.0 mm; 17, MZUSP; 7, USNM 216899, SL 12.2–20.5 mm; 7, CAS 39167, SL 11.8–20.5 mm; 8, MZUSP; 7, USNM 216908, SL 12.3–24.4 mm; 24, MZUSP; 9, USNM 216898, SL 10.4–22.6 mm; 6, BMNH 1977.4.20.11–16, SL 11.2–24.0 mm; 5, ZMA 115.065, SL 13.7–21.0 mm.—7, USNM 216907, SL 12.5–24.5 mm, Brazil, Amazonas, Rio Negro, São João near Tapurucuara (1°30′N, 65°2′W), 27 October 1972, Paulo Vanzolini for EPA.—With same data as USNM 216907 immediately preceding: 6, MZUSP; 6, USNM 216909, SL 13.1–24.5 mm.—17 alizarin preparations, USNM 216740, SL 13.6–24.2 and 10, USNM 216739, SL 20.2–24.8 mm, Brazil, Amazonas, "tributaries of upper Rio Negro," September–October 1975, from Cardinal Aquarium, Manaus, Brazil through Ross Socolof.—4, NRM THO/1977228.4088, SL 20.8–23.1 mm, Colombia, Guainia, Caño Bacon, pueblo Bretonia, about 3°39′N, 68°05′W, June 2–6, 1972, T. Hongslo.—11, NRM THO/197207.3049, SL 19.7–26.7, same locality data as preceding but collected May 27, 1972 by Hongslo.—7, NRM THO/1972230.3035, SL 14.5–16.7, Colombia, Guainia, Caño Bacon, Puerto Nariño, about 3°36′N, 68°15′W, June 6, 1972, T. Hongslo.—1, NRM THO/1972106.3133, SL 13.8 mm, Colombia, Vichada, Río Guarrojo, near its mouth, about 4°07′N, 70°45′W, March 11, 1972, T. Hongslo.—1, NRM THO/1972103.4155, SL 13.4 mm, same locality data as preceding but collected March 8, 1972.—2, NRM THO/1972103.3060, SL 11.8–12.5 mm, same data as preceding.—34, USNM 216903, SL 10.1–23.7 mm and 4 alizarin preparations, USNM 216916, SL 10.1–15.2 mm, Colombia, Vichada, Caño Muco (4°16′N, 70°20′W), 2 April 1974, J. E. Thomerson and party.—Following lots with same locality data as USNM 216903 immediately preceding: 15 alizarin preparations, MCZ 52459, SL 10.1–13.9 mm; 10, ANSP 138017, SL 10.9–13.2 mm; 10, BMNH 1977.4.20.1–10, SL 11.5–13.0 mm; 10, CAS 39147, SL 10.8–12.0 mm.—7, USNM 231737, SL 11.3–23.4 mm, Colombia, Vaupés, Río Vaupés at Mitú (1°7′N, 70°4′W), November 1964, H. R. Axelrod.—5, USNM 216756, SL 12.1–13.6 mm and 5, MBUCV-V 6095, Venezuela, Amazonas, small caño tributary to Rio Casiquiare near Beripomoni (2°4′N, 66°9′W), 28 January 1969, Antonio Machado and Jose Mosco.—6, USNM 216759, SL 22.2–27.5 mm, Venezuela, Amazonas, Caño Morocoto, Río Orinoco drainage, vicinity of San Fernando de Atabapo (4°4′N, 67°42′W), 13 February 1974, A. Cortez.—Following lots with same locality data as USNM 216759 immediately preceding: 6, MBUCV-V 9640, SL 23.4–27.1 mm; 4, ANSP 137965, SL 23.0–26.6 mm; 4, BMNH 1977.3.11.1–4, SL 22.2–28.3 mm; 5, MCZ 52341, SL 23.2–28.8 mm; 7, USNM 216760, SL 13.2–19.1 mm; 9, ANSP 137963, SL 13.2–16.5 mm; 9, MCZ 52340, SL 13.0–16.8 mm.—3, USNM 216897, SL 13.5–14.7 mm, Venezuela, Amazonas, caño near Sipapo (2°6′N, 66°28′W), left bank of Rio Casiquiare, 1 February 1969, Antonio Machado and Jose Mosco.—Following lots with same locality data as USNM 216897 immediately preceding: 3, MBUCV-V 6980, SL 13.4–16.5 mm; 3, ANSP 138019, SL 13.8–15.8 mm; 4 alizarin preparations, USNM 216914, SL 14.4–15.4 mm.—10, USNM 216754, SL 10.3–12.0 mm and 10, MBUCV-V 8017, Venezuela, Amazonas, Caño Caranaven, tributary to Rio Orinoco near San Fernando de Atabapo (4°4′N, 67°42′W), 4 December 1973, A. Cortez and R. Navarro.—2, USNM 216755, SL 13.9–14.3 mm, Venezuela, Amazonas, Caño Pamoni (2°50′N, 65°54′W), 28 Janaury 1969, Francisco Mago-Leccia, Antonio Machado, Jose Mosco.—121, USNM 236841, SL 11.0–25.9 mm, Brazil, Amazonas, tributary to Igarapé Tarumã Açu, about 20 km north of Manaus on road between Manaus and Itacoatiara (Serpa) (2°55′S, 60°00′W), 18 November 1979, Michael Goulding, Marilyn Weitzman, Stanley H. Weitzman (this locality is an introduction).—21 alizarin preparations, USNM 216910, SL 12.8–33.1 mm, locality unknown, aquarium specimens.—11, USNM 216904, SL 21.9–31.4 mm, locality unknown, aquarium specimens.

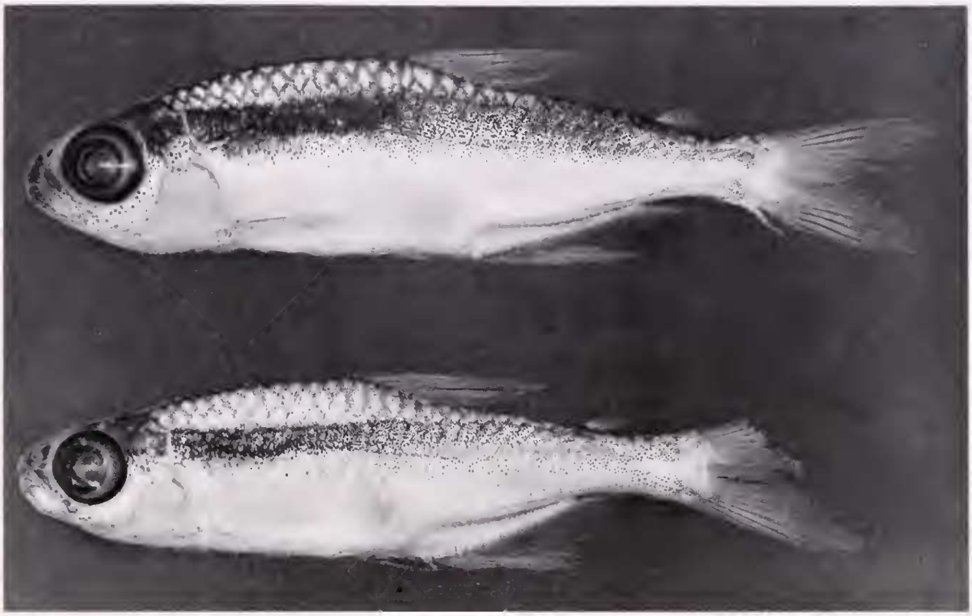

Figure 26. *Paracheirodon axelrodi,* Brazil, Amazonas, Rio Negro at São João near Tapurucuara, USNM 216905, female above, SL 24.6 mm, male below, SL 22.5 mm.

Paracheirodon axelrodi occurs in the upper Rio Negro region from the region of Tapurucuara west to at least the lower regions of the Río Vaupés in Colombia (=Rio Uaupes in Brazil), the Río Içana, the Río Guainia northward up the Rio Casiquiare in Venezuela and the headwater area of the Río Orinoco. It very probably occurs in the adjacent regions of the Río Sipapo and the Río Atabapo of Venezuela, and the Río Inirida, Río Guaviare, Río Vichada, and Río Meta of Colombia. This species has escaped and is reproducing in at least one stream, a tributary of the Igarapé Tarumã Açu, about 20 km north of Manaus. See Appendix 2 for discussion of the type locality.

Description. See Table 2 for morphometrics and meristics of individual population samples. Morphometrics given below are total ranges for all samples including some not in Table 2. Aquarium specimens are excluded.

Body moderately elongate, not compressed. Greatest body depth at or slightly anterior to dorsal-fin origin. Predorsal body profile moderately convex to area dorsal to eye. Body profile concave at nape. Body profile somewhat elevated at dorsal-fin origin; slightly convex or nearly straight along dorsal-fin base; slightly convex between dorsal-fin base and adipose-fin origin. Caudal peduncle concave in both dorsal and ventral profiles. Dorsal fin midway between caudal-fin base and snout tip or slightly nearer snout tip. Ventral body profile slightly convex from anterior tip of lower jaw to posterior anal-fin termination. In specimens which appear starved, Figure 29, belly profile may be nearly straight.

Head and snout relatively short, snout blunt. Mouth nearly terminal with lower jaw slightly included when mouth fully closed. Gape angled somewhat anterodorsally from mandibular joint to snout tip. When mouth closed, maxilla extends posteriorly to a point approximately on a vertical line drawn ventrally from anterior border of pupil.

Dorsal-fin rays ii-8 to ii-9, usually ii-9, n = 91; adipose fin present; anal-fin rays

TABLE 2. MORPHOMETRICS AND MERISTICS OF *Paracheirodon axelrodi*.†

		Venezuela, Morocoto					Colombia, Caño Muco					Brazil, Tapurucuara					Total R	
			Range					Range					Range					
	Holotype	*n	Low	High	X̄	SD	n	Low	High	X̄	SD	n	Low	High	X̄	SD	Low	
Standard length	22.0	7	11.6	18.5	14.4		18	11.0	23.4	13.3		59	10.5	25.1	17.7		10.5	25.1
Greatest body depth	31.8	7	23.7	27.6	25.8	1.513	18	26.4	30.1	28.3	1.028	59	24.0	30.7	27.3	1.644	23.7	30.9
Snout to dorsal-fin origin	52.7	7	50.7	54.3	52.5	1.252	18	52.1	54.9	53.3	0.814	59	50.3	56.0	52.7	1.049	50.3	56.0
Snout to pectoral-fin origin	26.4	7	27.6	31.9	30.1	1.606	18	26.9	32.0	30.7	1.344	59	26.8	34.4	30.3	1.818	26.4	34.4
Snout to pelvic-fin origin	50.5	7	48.6	50.7	49.4	0.780	18	49.2	54.3	50.6	1.159	59	46.3	52.6	49.0	1.204	46.3	54.3
Snout to anal-fin origin	66.4	7	61.8	65.9	64.4	1.389	18	61.2	65.4	63.8	0.965	59	59.8	67.2	63.6	1.313	59.8	67.2
Eye to dorsal-fin origin	36.8	7	34.3	36.0	35.3	0.581	18	34.8	37.3	35.9	0.790	59	33.5	39.8	35.8	1.354	33.5	39.8
Dorsal-fin origin to caudal-fin base	55.5	7	49.1	52.5	50.6	1.125	18	50.0	54.6	51.8	1.237	59	49.0	55.2	52.0	1.240	49.0	55.5
Caudal-peduncle depth	10.5	7	8.0	12.0	9.6	1.353	18	9.4	10.9	10.1	0.358	59	8.3	10.3	9.3	0.502	8.0	12.0
Caudal-peduncle length	14.5	7	15.3	16.8	16.0	0.512	18	14.4	16.7	15.6	0.597	59	14.8	18.6	16.5	0.750	14.5	18.6
Pectoral-fin length	—	4	17.6	19.8	19.0	1.017	16	15.7	19.7	17.9	1.146	54	16.2	23.8	19.3	1.497	15.7	23.8
Pelvic-fin length	15.5	7	13.5	16.8	14.9	1.538	18	14.1	17.5	16.1	0.733	58	13.4	21.8	17.3	1.630	13.4	21.8
Dorsal-fin base length	14.4	7	12.7	13.9	13.5	0.443	18	12.7	14.8	14.0	0.572	59	12.0	15.2	13.6	0.660	12.0	15.2
Longest dorsal-fin ray length	27.3	6	27.2	28.4	28.0	0.450	15	26.8	30.4	28.5	1.031	55	25.7	33.0	28.6	1.508	25.7	33.0
Anal-fin base length	23.2	7	22.4	23.7	23.0	0.486	18	22.1	25.5	23.7	0.887	59	21.7	26.0	23.9	0.963	21.7	26.0
Longest anal-fin ray length	20.5	2	23.2	23.9	23.6	0.495	14	22.6	25.8	24.1	1.000	56	21.9	26.3	23.9	1.022	20.5	26.3
Bony head length	25.9	7	26.5	30.2	28.3	1.421	18	25.2	30.2	28.9	1.086	59	24.7	32.2	28.2	1.714	24.7	32.4
Horizontal eye diameter	40.4	7	40.8	45.7	43.4	1.506	18	40.7	48.6	44.2	1.682	59	39.1	45.9	42.2	1.508	39.1	45.9
Snout length	19.3	7	16.7	19.4	18.0	0.911	17	13.9	20.3	17.2	1.507	59	16.2	23.0	19.4	1.570	13.9	23.0
Least bony inter-orbital width	28.1	7	25.0	27.0	26.0	0.675	17	25.0	29.7	27.2	1.472	58	22.0	30.4	26.2	1.898	22.0	30.4
Upper jaw length	35.1	7	30.6	33.3	31.3	0.945	16	28.2	32.4	30.5	1.267	58	24.5	39.5	32.0	2.573	24.5	39.5
Branched dorsal-fin rays	9	13	8	9	8.8	0.376	18	9	9	9	0.000	48	8	9	8.9	0.309	8	9
Branched pectoral-fin rays	11	13	10	11	10.2	0.439	18	10	11	10.8	0.428	48	10	11	10.6	0.483	10	11
Branched pelvic-fin rays	7	13	7	7	7	0.000	18	7	7	7	0.000	48	7	7	7	0.000	7	7
Branched anal-fin rays	17	13	14	17	16.0	0.707	18	15	17	16.2	0.618	48	15	19	16.6	0.841	14	19

TABLE 2. CONTINUED.

		Venezuela, Morocoto					Colombia, Caño Muco					Brazil, Tapurucuara					Total R	
			Range					Range					Range					
	Holotype	*n	Low	High	X̄	SD	n	Low	High	X̄	SD	n	Low	High	X̄	SD	Low	
Horizontal scale rows between dorsal fin and pelvic fin	9	8	9	9	9	0.000	3	9	9	9	0.000	43	9	9	9	0.000	9	9
Predorsal scales	—	13	9	10	9.4	0.506	4	9	9	9	0.000	26	9	11	9.9	0.628	9	11
Perforated lateral-line scales	7	7	5	7	6.0	0.577	1	6	6	—	—	26	5	8	6.5	0.762	5	8
Lateral series scales	31	7	30	33	31.0	1.000	1	31	31	—	—	22	30	32	31.3	0.767	30	33
Horizontal scale rows around caudal peduncle	12	8	12	12	12	0.000	1	12	12	—	—	26	12	12	12	0.000	12	12
Dorsal-limb gill rakers	7	13	6	8	6.9	0.641	18	6	7	6.7	0.461	35	6	8	7.1	0.404	6	8
Ventral-limb gill rakers	12	13	12	14	12.8	0.555	18	12	14	12.6	0.608	36	11	13	12.3	0.535	11	14
Vertebrae	32	12	31	33	32.0	0.426	18	31	33	32.1	0.416	64	31	33	32.2	0.420	31	33

† Holotype USNM 104483; Rio Morocoto, Venezuela, USNM 216760, USNM 216759; Caño Muco, Colombia, USNM 216903; Tapurucuara, Brazil, USNM 216901, USNM 216900, USNM 216905, USNM 216902, USNM 216899, USNM 216898, USNM 216908, USNM 216907, USNM 216909, USNM 216740, ANSP 138018, MCZ 52460, MCZ 52461, CAS 39167, ZMA 115.065, BMNH 1977.4.20.11–16. Standard length is expressed in mm. The next 16 measurements (through head length) are percentages of standard length. The next four measurements are percentages of bony head length.

* Six specimens were raised to adult size in an aquarium and were not included in the measurements.

iii-14 to iii-19, usually iii-16 or iii-17, n = 91; pectoral-fin rays i-10 to i-11, usually i-11, n = 91; pelvic-fin rays i-7, n = 91; and caudal-fin rays 10/9, n = 91. Bony pelvic-fin hooks present in mature male specimens equal to or longer than 17.3 mm SL; some immature males between 17.0 and 19.5 mm SL without hooks, all males longer than 19.5 mm SL mature and with pelvic-fin hooks.

Scales cycloid. Lateral line incomplete; perforated lateral-line scales 5 to 8, usually 6 or 7, n = 35; scales in a lateral series 30 to 33, usually 31, n = 31; scale rows between anterior dorsal-fin base and pelvic-fin base 9, n = 55; predorsal scales 9 to 11, usually 10, n = 41; horizontal scale rows around caudal peduncle 12, n = 36.

Dorsal-limb gill rakers 6 to 8, usually 7, n = 67; ventral-limb gill rakers 11 to 14, usually 12 or 13, n = 67.

Total number of vertebrae including Weberian apparatus and terminal compound centrum 31 to 33, usually 32, n = 77.

Dental Morphology. A single row of five premaxillary teeth, each with five cusps, is present in adults (Fig. 20A,B). Specimens of about 10 mm SL have five to six tricuspid teeth (Fig. 20C). During ontogeny replacement teeth usually have four or five cusps (Fig. 20D), with the adult configuration of cusps reached at about 18 mm SL. Specimens smaller than this size have five to six premaxillary teeth; specimens larger consistently have five teeth. Cusp number is not increased with increased SL in available specimens caught in the wild. A single maxillary tooth with five cusps usually is present in adult *P. axelrodi* (Fig. 20B). Ontogenetic replacement of teeth with fewer cusps by teeth with more cusps occurs as with the premaxillary teeth (compare Fig. 20B,D). Juveniles of about 10 mm SL lack maxillary teeth (Fig. 20C). Our small sample of wild-caught juveniles shows teeth with one to three cusps in fishes 11 to 15 mm SL, four to five cusps in fishes 16 to 18 mm SL, and five cusps in specimens larger than 18 mm SL.

Dentary teeth lie in a single row, numbering 5 to 11, usually 7 or 8. The anteromedial three or four teeth are largest, with three to seven, usually five, cusps; laterally successive teeth are smaller, with concommitant decrease in cusp number (Fig. 20E,F). In specimens available to us, there is a slightly smaller total cusp number per dentary tooth in specimens less than about 14 mm SL than in larger specimens, indicating ontogenetic replacement by teeth with a greater number of cusps. We found no apparent correlation of dentary tooth number and SL.

Color Pattern. In life *P. axelrodi* (Fig. 2) back dark olive brown with reticulate dark chromatophore pattern, as described under color in alcohol, below. Intense iridescent blue to blue-green lateral stripe extends from skin over anterior infraorbital bones, over cornea of eye (usually concentrated dorsally), sparsely over cheeks, over opercle, and posteriorly to just ventral to posterior border of adipose fin. Blue lateral stripe broadest just anterior to a vertical from dorsal-fin origin. Dense stripe of black chromatophores visible dorsal to blue stripe, broadest in area between opercle and dorsal-fin origin. Broad stripe of loosely scattered dark chromatophores present ventral to blue lateral stripe, but usually not visible because of red pigment. Numerous erythrophores over sides of body ventral to blue stripe, extending ventrally approximately to a line between pectoral-fin origin and anus anteriorly and to anal-fin base and ventral border of caudal peduncle posteriorly. Numerous erythrophores also present anteriorly over ventral portion of opercle and posteriorly over dorsum of caudal peduncle, scales at caudal-fin base, and dorsally to ventral border of blue lateral stripe. In disturbed individuals with erythrophores contracted, very narrow stripe of pale brown present between blue lateral stripe and red area. Erythrophores immediately dorsal to anal-fin base slightly less dense than in rest of red stripe; this area defined dorsally by narrow stripe of dark chromatophores extending to ventral border of caudal-fin base. Belly silvery white ventral to erythrophore area, reflecting blue under some light conditions. Fins hyaline except for faint white area along anterior anal-fin rays; indistinct whitish area along anterior border of dorsal fin and white area on adipose fin in some specimens.

Compared to *P. simulans*, *P. axelrodi* has a bluer stripe which posteriorly terminates ventral to the adipose fin, less blue on eye, and more intense red pigmentation over a wider area of the body. See also the live color description of *P. simulans.*

Compared to *P. innesi*, *P. axelrodi* has a slightly wider and longer blue stripe, much more widely distributed red pigment, and less distinct white markings on the anal fin. See also the live color description of *P. innesi.*

In alcohol *P. axelrodi* (Fig. 26) with ground color light cream brown. Scale pocket margins of dorsum and two ventrally successive lateral scale rows lined with light brown chromatophores, giving a reticulate pattern. Small brown chromatophores may lie scattered within scale pocket areas defined by marginal chromatophores. Midlateral stripe consists of two kinds of chromatophores: dense dark-brown chromatophores extend from just posterior to eye (where they extend onto dorsum of head, see below) to just ventral to adipose fin, lying along myosepta in that area; lighter brown, less dense and less numerous chromatophores lie just ventral to darker ones, extending from just posterior to opercle to caudal-fin base and slightly onto upper and lower caudal-fin lobes. Dorsal border of lateral stripe lies about two to two and a half scale rows ventral to dorsal-fin origin; maximum width of lateral stripe about two to two and a half scales. Small brown chromatophores may occur sparingly over belly and flanks dorsal to anal fin. Small dark chromatophores lie along anal-fin base and along a line marking conjunction of anal-fin musculature and hypaxial body musculature. Dark brown chromatophores cover head dorsally, extending anteriorly over tips of upper and lower jaws and posteriorly onto dorsum of body to caudal-fin base as thin line marking dorsal midline. Large dark chromatophores in area of infraorbital probably represent anterior extension of lateral stripe. Dark chromatophores distributed sparingly over infraorbital and preopercular area. A few dark chromatophores form a very thin margin on ventral border of orbit. Small chromatophores line fin-ray borders of all fins; interradial membranes without chromatophores. Adipose fin with small dark chromatophores, concentrated about at center of fin.

Specimens from MCZ 52241 exhibit much the same pigment patterns as those in MCZ 52460, but two kinds of chromatophores are not evident in lateral dark stripe. Densely arranged dark chromatophores extend posteriorly only to anterior of adipose-fin base; less numerous, usually smaller chromatophores extend posteriorly to caudal-fin base (becoming larger and more numerous posteriorly). Dark chromatophores also form a line over anal-fin base to ventral portion of caudal-fin base. Small dark chromatophores occur sparingly over ventral border of caudal peduncle, but these not organized into a stripe.

Specimens from MCZ 52459 much less pigmented than those described above. In these, dark chromatophores restricted almost entirely to head (as described above), dense lateral stripe (only one kind of chromatophore evident) which extends only to vertical from anal-fin origin, a few scale margins of dorsum, and along fin-ray borders.

Population Variation. For the most part our sample sizes are small and not suitable for studies of intraspecific variation. How-

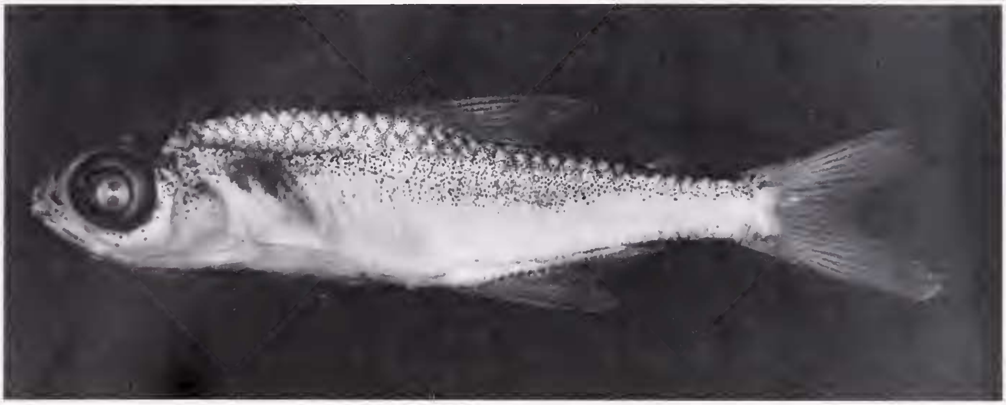

Figure 27. *Paracheirodon innesi*, Colombia, Amazonas, Rio Loreto Yacu, male, SL 22.2 mm, MCZ 52156.

ever, some variation appears evident in the numbers of fin rays, scales, and gill rakers. As an example, using a two-tailed test and square root transformations in computing value of t, we found significant differences ($P < 0.01$) in numbers of branched pectoral-fin rays, branched anal-fin rays, predorsal scale number, and ventral-limb gill raker counts in population samples from Tapurucuara, Rio Negro, Amazonas, Brazil (n = 48) and Morocoto, Río Orinoco, Amazonas, Venezuela (n = 13). A study of the significance of this sort of variation in *P. axelrodi* in relation to geographic distribution must await intensive collections of samples throughout its range.

Paracheirodon innesi (Myers)

Figures 3, 8, 21, 22, 23, 24B, 27; Tables 3 to 7

Hyphessobrycon innesi Myers, 1936: 97, original description, Peru, "near Iquitos" (see discussion, Appendix 2).—Innes, 1936: 135, introduction into aquarium trade and source of type specimens.—Stoye, 1936: 137, type locality based on interview with collector August Rabaut.—Myers and Weitzman, 1956: 2, relationships.—Hoedeman, 1956: 154, relationships.—Géry, 1960b: 9, relationships.—Lueken and Foerster, 1969: 174, chromosome study.

Paracheirodon innesi (Myers), Géry, 1960b: 12, relationships, referral to new genus.—Géry, 1963: 70, relationships.—Post, 1965: 65, chromosome numbers.—Scheel and Christensen, 1970: 24, relationships based on chromosomes.—Scheel, 1972: 60, relationships based on chromosomes.—Géry, 1977: 587, relationships.

Cheirodon innesi (Myers), Van Ramshorst, 1981: 142, aquarium description, referral of *P. innesi* to *Cheirodon*.

Specimens Examined. Holotype, USNM 102109, SL 22.2 mm; Colombia, Amazonas, somewhere up the Río Putumayo, March–April 1936, August Rabaut. [Note: original type locality listed by Myers (1936) as "near Iquitos" in Peru was later discussed by Stoye (1936) and noted to be Río Putumayo in Colombia].—29, USNM 216699, SL 13.1–18.5 mm, Colombia, Amazonas, Río Loreto Yacu, in small creeks about 1 km from mouth of Río Loreto Yacu where it empties into Río Marañon (3°30′S, 70°10′W), 3 December 1976, Alfonso Doaz.—71 (13 of these alizarin preparations), MCZ 52156, SL 13.4–22.2 mm, same locality data as USNM 216699.—1, MCZ 52165, SL 18.5 mm, Colombia, Amazonas, small tributary of Lago Yahuacaca (4°5′S, 69°58′W) on Río Marañon (=Río Amazonas), December 1976, W. L. Fink.—1, USNM 216865, SL 19.1 mm, Colombia, Amazonas, near Leticia (4°14′S, 69°55′W), 4 December 1974, Donald Kramer.—1, MZUSP 13256, SL 14.3 mm, Brazil, Amazonas, Lago Miuá (3°48′S, 62°12′W), connecting with Rio Solimões somewhat west of Codajás, 25 September 1968, EPA.—8, USNM 216710, SL 12.6–15.0 mm, Brazil, Amazonas, near Rio Tapauá where it enters Rio Purus (5°45′S, 64°20′W), November 1963, H. R. Axelrod, H. Schultz, F. Terofal.—16, USNM 216912, SL 12.9–26.5 mm, aquarium specimens, 1974 (alizarin preparations).—10, USNM 216906, SL 23.6–25.5 mm, aquarium specimens, 1975.—28, NRM THO/1971371.3220, SL 13.3–16.3 mm, Brazil, Amazonas, Rio Javari, Lago Guariba, Caño de Guariba, about 4°12′S, 70°17′W, September 13, 1971, T. Hongslo.

The confirmed range of this species is in two disjunct areas. One is the area around Leticia and Tabatinga, in the lower course of the Rio Putumayo, and in small streams entering the Rio Solimões a few km downstream from Leticia. The second area is about 870 straight-line km east of the first region, near Codajás, and at least 400 straight-line km up the Rio Purus, a large river emptying into the Rio Solimões about 75 km east of Codajás. We doubt that the actual distribution of *P. innesi* is disjunct and we presume that *P. innesi* may have a wide distribution in western Brazil in tributaries along the Rio Solimões, in southeastern Colombia and in eastern Peru along the lowland tributaries of the Río Napo and the Río Putumayo which, as the Rio Iça, enters the Rio Solimões in Brazil. Sven Kullander, personal communication, states that *P. innesi* is present in the area around Janaro Herrrera (4°55′S, 73°40′W) on the Río Ucayali of Peru. Harald Schultz (1962: 43) reported neon tetras ". . . from the Japura . . . southward to the region of Iquitos." He stated that neon tetras are found in all flowing blackwater streams of this region. Geisler (1979: 24) reported neon tetras from the Río Curaray, a tributary of the Río Napo in Peru. These last two localities are not represented by specimens in museums. In areas where *P. innesi* occurs it is always in blackwater or clearwater streams and is never found in whitewater streams with their headwaters in the Andes. This species is often temporarily held in aquarium compounds in diverse areas of South America. Its successful introduction into some of these areas with the proper ecological conditions may be inevitable and should be carefully screened for future zoogeographic considerations. See Appendix 2 for discussion of the type locality.

Description. See Table 3 for morphometrics and meristics of holotype and one population sample. Morphometrics given below are total ranges for all samples examined except aquarium specimens.

Body moderately elongate, not compressed. Greatest body depth at or slightly anterior to dorsal-fin origin. Predorsal body profile moderately convex to area dorsal to eye, sometimes concave at the nape. Body profile slightly elevated at dorsal-fin origin; slightly convex along dorsal-fin base; slightly convex between dorsal-fin base and adipose-fin origin. Caudal peduncle profile somewhat concave in both dorsal and ventral profiles or ventral one nearly straight. Dorsal fin midway between caudal-fin base and snout tip or nearer snout tip than caudal-fin base. Ventral body profile convex from anterior tip of lower jaw to posterior anal-fin termination. Often nearly straight between posterior tip of lower jaw and anus in wild-caught specimens (Fig. 27).

Head and snout relatively short with a blunt, rounded snout. Mouth terminal. Gape angled somewhat anterodorsally from mandibular joint to snout tip. Maxilla extends posteriorly to a point approximately on a vertical line drawn ventrally from anterior border of pupil.

Dorsal-fin rays ii-8 to ii-9, usually ii-9, n = 22; adipose fin present; anal-fin rays iii-16 to iii- or iv-19, usually iii-16 or iii-17, n = 22; pectoral-fin rays i-11 to i-13, usually i-12, n = 22; pelvic-fin rays i-6 to i-7, usually i-7, n = 22; caudal-fin rays 10/9, n = 22. Bony pelvic-fin hooks absent in all specimens.

Scales cycloid. Lateral line incomplete; perforated lateral-line scales 3 to 6, usually 5, n = 22; scales in a lateral series 30 to 33, usually 31, n = 21; scale rows between anterior dorsal-fin base and anterior pelvic-fin base 9, n = 21; predorsal scales 9 to 11, usually 10, n = 21; horizontal scale rows around caudal peduncle 12, n = 21.

Dorsal-limb gill rakers 5 to 6, either 5 or 6, n = 21; ventral-limb gill rakers 10 to 11, usually 11, n = 21.

Total number of vertebrae including Weberian apparatus and terminal compound centrum 32 to 34, usually 33, n = 30.

Dental Morphology. There is greater variation in tooth placement in *P. innesi* (Figs. 21–23) than in *P. simulans* or *P. axelrodi*. Géry (1960b: 9), noted the usual condition in wild-caught specimens as a slightly irregular series of six or seven tricuspid teeth (we find a rare count of eight), with one or more teeth offset somewhat anteriorly to other teeth of the row (Fig. 21A–D). The anteriorly-set teeth were interpreted by Myers (1936: 97) as a second row and by Géry (1960b: 9) as members of a "wavy" single tooth row. To determine whether either hypothesis should be rejected, we examined a large series of specimens, both wild caught and from the aquarium trade. Recently imported

TABLE 3. MORPHOMETRICS AND MERISTICS OF *Paracheirodon innesi*.†

	Holotype	Brazil, Amazonas (n = 1 or 0)	Colombia, Lago Yahuacaca				
				Range			
			n	Low	High	$\bar{X}$	SD
Standard length	21.4	14.3	20	13.9	22.2	16.6	
Greatest body depth	35.0	28.0	20	22.7	28.8	26.2	1.392
Snout to dorsal-fin origin	54.2	53.0	20	49.7	54.7	52.6	1.092
Snout to pectoral-fin origin	27.1	31.5	20	28.4	32.5	30.7	1.014
Snout to pelvic-fin origin	49.5	51.7	20	45.5	50.0	47.7	1.099
Snout to anal-fin origin	64.0	62.2	20	56.2	63.1	61.1	1.581
Eye to dorsal-fin origin	37.4	36.4	20	33.0	37.5	35.3	0.960
Dorsal-fin origin to caudal-fin base	52.3	50.3	20	50.3	53.8	51.7	0.929
Caudal peduncle depth	10.7	9.8	20	8.8	10.6	9.8	0.467
Caudal peduncle length	16.4	17.5	20	14.8	18.0	16.0	0.784
Pectoral-fin length	17.8	—	20	17.8	20.3	19.1	0.739
Pelvic-fin length	16.8	—	20	15.8	18.8	17.3	0.775
Dorsal-fin base length	—	13.3	20	12.5	14.4	13.5	0.620
Longest dorsal-fin ray length	23.8	—	19	25.5	30.2	28.7	1.074
Anal-fin base length	23.4	24.5	20	24.1	26.5	25.2	0.666
Longest anal-fin ray length	25.7	—	19	22.7	25.6	24.7	0.692
Bony head length	28.0	28.7	20	27.0	29.9	28.6	0.905
Horizontal eye diameter	45.5	43.9	20	40.0	45.5	43.1	1.409
Snout length	18.2	19.5	20	15.9	20.9	18.7	1.174
Least bony interorbital width	29.1	31.7	20	26.7	34.7	29.1	1.998
Upper jaw length	36.4	31.7	20	29.4	34.9	31.9	1.676
Branched dorsal-fin rays	8	9	20	9	9	9	0.000
Branched pectoral-fin rays	12	11	20	11	13	11.8	0.550
Branched pelvic-fin rays	7	6	20	6	7	6.9	0.308
Branched anal-fin rays	17	17	20	16	18	17.5	0.889
Horizontal scale rows between dorsal fin and pelvic fin	9	—	20	9	9	9	0.000
Predorsal scales	10	—	20	9	11	10.0	0.549
Perforated lateral-line scales	9	—	29	3	6	4.6	0.940
Lateral series scales	33	—	20	30	33	31.3	0.933
Horizontal scale rows around caudal peduncle	12	—	20	12	12	12	0.000
Dorsal-limb gill rakers	5	—	20	5	6	5.5	0.513
Ventral-limb gill rakers	11	—	20	10	11	11	0.224
Vertebrae	33	—	29	32	34	33	0.267

† Holotype, USNM 102109; Lago Miua, Amazonas, Brazil, MZUSP 13256; Lago Yahuacaca, Colombia, USNM 216699. Standard length is expressed in mm. The next 16 measurements (through head length) are percentages of standard length. The next four measurements are percentages of bony head length.

aquarium specimens have tooth-row patterns like those of wild-preserved fishes, but some specimens kept in aquaria for several months or years develop tooth distribution irregularities (discussed below); this may be related to the flake-food diet of aquarium specimens, or it may be a factor of age.

We find most wild-preserved *P. innesi* to have one or two teeth offset slightly anterior to the main tooth row. In our sample of *P. innesi* from near Leticia, Colombia (USNM 216699 and MCZ 52156) the third tooth from the premaxillary symphysis is offset in about 70 percent of the specimens examined, the fourth tooth is offset in about 20 percent, and the second and fifth teeth each are offset in about 10 percent. Rarely, two teeth are offset on the same premaxillary bone. These two teeth usually are the second and fourth, or third and fifth from the symphysis.

Body size apparently is not correlated with the number of teeth offset from the main row.

We find, with rare, notable exceptions, that the anteriorly offset teeth lack developed main-row teeth posterior to them. Their replacement teeth are present either in series with other replacement teeth or offset slightly anterior to the replacement tooth row (Figs. 21A, 23B).

While in most cases an anteriorly offset tooth of *P. innesi* cannot be called a "true" outer-row tooth, we find that some individuals retain a degree of genetic lability regarding tooth rows. An example is a wild-preserved specimen 13.5 mm SL (from MCZ 52156) with six teeth on each premaxilla (Fig. 22) and with the third tooth from the symphysis on each bone offset slightly anteriorly and conical rather than tricuspid. While the tooth on the left side clearly has one cusp (Fig. 22), the tooth on the right side (not illustrated) has tiny lateral protrusions which may represent underdeveloped cusps. On the left premaxilla of this specimen all the tricuspid teeth have tricuspid replacement teeth posterior to them; the replacement tooth for the anterior conical tooth lies slightly anterior to the rest of the replacement tooth row and has a single, elongate cusp. On the right premaxilla, the tooth nearest the symphysis had just moved into a functional position when the fish was preserved and its base is not fully developed; the second tooth also has a partially-emplaced replacement tooth. The conical tooth has what may be a forming replacement tooth, represented by a tiny mineralized element, lying anterodorsal to the other parts of the replacement tooth row. The fourth tooth from the symphysis is a replacement tooth almost in its functional position, and the fifth tooth is a partially-formed tricuspid replacement tooth.

Two aquarium specimens examined also are pertinent to this discussion. A *P. innesi* specimen purchased as an imported wild specimen and raised to 25.7 mm SL shows a single conical tooth set somewhat anterior to the other premaxillary teeth, with a tricuspid tooth posterior to it (Fig. 23A,C). This conical tooth may be a worn tricuspid tooth about to be replaced by a newly formed tricuspid tooth, or it may be a true, if somewhat misshapen, conical tooth being replaced. The second specimen, which lived for about four years in an aquarium, exhibits extraordinary tooth morphology (Fig. 23B,D). The medial two and lateral two teeth are positioned as usual, but between them there is a series of one conical and five tricuspid teeth. Perhaps most important to our discussion is the presence of a conical tooth set anteromedial to the two normally placed lateral teeth. This conical tooth is fully formed and sharply pointed, not a worn-down tricuspid tooth as may be the case in the previously discussed specimen. Posterior to this conical tooth is a replacement tooth in its own trench, situated anterior to the other replacement teeth. This condition is that seen in *P. simulans* which has a true second tooth row (Fig. 21A,B,D). While it is doubtful that wild fishes ever reach the age of this particular specimen, and while abnormal habitat and/or diet might have been partially responsible for the very unusual tooth arrangement, this specimen does demonstrate that the genetic potential for a second premaxillary tooth row remains in *P. innesi*.

We conclude that while in most specimens there is a "wavy" premaxillary tooth line, the potential remains, in some specimens, for a second tooth row to develop. Teeth of the premaxilla are not replaced simultaneously, but at least one or two teeth seem to be replaced out of synchrony with others. The sample size available is insufficient to determine replacement patterns.

The maxillary teeth in *P. innesi* number two to three, usually three, with three cusps on each tooth (Figs. 21C,D; 23C,D). In the old aquarium-raised specimen discussed above (Fig. 23D), a single conical tooth is present on the maxilla somewhat distal to the tricuspid teeth. Other aquarium-raised specimens have one to four, usually two, maxillary teeth (n = 16; 12.9–26.5 mm SL).

Dentary teeth in *P. innesi* usually number six to nine, with the more medial teeth tricuspid and those lying more laterally and posteriorly are conical. We found no statistically significant increase in tooth cusp number with increased body size. Figures 21F and 23E are representative of dentary tooth morphology.

Color Pattern. In life, *P. innesi* (Fig. 3) back dark olive brown with reticulate dark chromatophore pattern as described in more detail below under color in alcohol. Intense iridescent blue-green lateral stripe extends from skin over anterior infraorbital bones, over cornea of eye (usually concentrated dorsally), sparingly over cheeks, over opercle, and posteriorly to within one to three scales anterior to adipose-fin base. Blue lateral stripe broadest in area approximately between dorsal and pelvic fins. Dense stripe of dark chromatophores dorsal to blue lateral stripe, broadest in area between opercle and dorsal-fin origin. Broad stripe of loosely scattered dark chromatophores ventral to blue lateral stripe. Numerous erythrophores cover area extending to a point about on a vertical from dorsal-fin origin anteriorly, posteriorly over scales of caudal-fin base, dorsally to just ventral to blue lateral stripe (and with a few erythrophores to dorsum of caudal peduncle in some individuals), and ventrally to anal-fin base. Side in area immediately ventral to blue lateral stripe without erythrophores; width of this apigmented area broadest in disturbed individuals, very narrow in undisturbed fish. Area of fewer erythrophores immediately dorsal to anal-fin base; this area defined dorsally by narrow stripe of dark chromatophores extending to ventral border of caudal-fin base. Belly silvery white, reflecting light blue ventrally under some light conditions. Fins hyaline except for distinct white stripe along anterior anal-fin rays, concentrated between posterior unbranched ray and anterior branched ray; indistinct whitish area along anterior border of dorsal fin and small white area in center of adipose fin in some specimens.

Compared to *P. simulans*, *P. innesi* with a bluer lateral stripe which extends only to adipose fin, more red on flanks, less blue on eye and face, and a much more distinct white line on anal fin. See also color description of *P. simulans*.

Compared to *P. axelrodi*, *P. innesi* with less red on belly and flank area, a somewhat narrower blue lateral stripe which extends less far posteriorly, and a much more distinct white line on anal fin. See also life color description of *P. axelrodi*.

In alcohol, *P. innesi* (Fig. 27) with ground color light cream brown. Scale pocket margins of dorsum and ventrally successive lateral scale rows lined with dark brown chromatophores. Small brown chromatophores may be scattered within scale pocket areas defined by marginal chromatophores. Midlateral stripe extends posteriorly from just posterior to eye to near adipose-fin base, then either terminating or becoming abruptly less dense and continuing along dorsal half of caudal peduncle as far as squamation of caudal-fin base. Dorsal border of lateral stripe lies about two and a half scale rows ventral to dorsal-fin origin; maximum width of lateral stripe about one to two scales. Belly usually non-pigmented. Peritoneum with numerous dark chromatophores, more obvious in smaller specimens. Dark chromatophores lie along anal-fin base and along line marking conjunction of anal-fin musculature and hypaxial body musculature; these lines converge at posterior termination of anal-fin base. In some specimens, scale pocket margins along ventral midline of caudal peduncle with dark chromatophores. Large dark chromatophores on area of infraorbital 1 are probably an anterior continuation of lateral stripe. Numerous small dark chromatophores over tips of jaws and dorsum of head, these extending posteriorly as a diffuse thin line to caudal-fin base, marking

TABLE 4. SIMILARITIES AND DIFFERENCES AMONG DORSAL-LIMB GILL RAKER COUNTS OF POPULATION SAMPLES OF THREE SPECIES OF *Paracheirodon*.†

	n	Range		$\bar{X}$	SD	t	P
Comparison between:							
P. simulans, Puerto Correño	42	5	6	5.9	0.328	14.626	**
P. axelrodi, Tapurucuara	35	6	8	7.1	0.404		
P. simulans, Puerto Correño	42	5	6	5.9	0.328	7.638	**
P. axelrodi, Rio Morocoto	13	6	8	6.9	0.641		
P. simulans, Puerto Correño	42	5	6	5.9	0.328	7.742	**
P. axelrodi, Caño Muco	18	6	7	6.7	0.461		
P. simulans, Puerto Correño	42	5	6	5.9	0.328	3.526	**
P. innesi, Lago Yahuacaca	20	5	6	5.5	0.513		
P. innesi, Lago Yahuacaca	20	5	6	5.5	0.513	12.960	**
P. axelrodi, Tapurucuara	35	6	8	7.1	0.404		
P. innesi, Lago Yahuacaca	20	5	6	5.5	0.513	7.015	**
P. axelrodi, Rio Morocoto	13	6	8	6.9	0.641		
P. innesi, Lago Yahuacaca	20	5	6	5.5	0.513	7.560	**
P. axelrodi, Caño Muco	18	6	7	6.7	0.461		
P. axelrodi, Tapurucuara	35	6	8	7.1	0.404	3.215	**
P. axelrodi, Caño Muco	18	6	7	6.7	0.461		
P. axelrodi, Tapurucuara	35	6	8	7.1	0.404	1.272	NS
P. axelrodi, Rio Morocoto	13	6	8	6.9	0.641		
P. axelrodi, Caño Muco	18	6	7	6.7	0.461	0.999	NS
P. axelrodi, Rio Morocoto	13	6	8	6.9	0.641		

† Square-root transformations were used in computing the value of t. Two-tailed test; * indicates $P < 0.05$; ** indicates $P < 0.01$; NS (not significant) indicates $P > 0.05$.

dorsal midline. Small dark chromatophores line fin-ray borders; interradial membranes without chromatophores. Adipose fin with or without small dark chromatophores.

DISCUSSION

The most obvious differences among the neon tetras are expressed in the key to the species. Tables 4 to 7 express statistical differences and similarities in counts of the dorsal and ventral limb gill rakers, perforated lateral-line scales, and branched anal-fin rays among population samples of the three neon tetra species. These tables show highly significant count differences among the species and in some instances between population samples of *P. axelrodi*. Other counts, except those used in the key, were essentially the same. Differences in tooth patterns, color pattern, and orbital bones are described either in the key, the descriptions of the species, or both. *Paracheirodon simulans* has several morphometric characters which may distinguish it from the other two species. These are a proportionately shorter dorsal-fin base length (probably a factor of its fewer fin rays), a shorter longest fin ray in the dorsal fin, a relatively short anterior anal-fin lobe, a relatively longer upper jaw, shorter head length; also, the distance between the posterior border of the eye and the dorsal-fin origin is longer relative to the distance between the dorsal-fin origin and the caudal-fin base. Among these three species most of these characters overlap in their ranges. Although our analyses of these apparent differences have shown some to be significant, they are not presented here because our measurements of

TABLE 5. SIMILARITIES AND DIFFERENCES AMONG VENTRAL-LIMB GILL RAKER COUNTS OF POPULATION SAMPLES OF THREE SPECIES OF *Paracheirodon*.†

	n	Range		$\bar{X}$	SD	t	P
Comparison between:							
P. simulans, Puerto Correño	42	10	12	11.2	0.484	9.485	**
P. axelrodi, Tapurucuara	36	11	13	12.3	0.535		
P. simulans, Puerto Correño	42	10	12	11.2	0.484	9.943	**
P. axelrodi, Rio Morocoto	13	12	14	12.8	0.555		
P. simulans, Puerto Correño	42	10	12	11.2	0.484	9.234	**
P. axelrodi, Caño Muco	18	12	14	12.6	0.608		
P. simulans, Puerto Correño	42	10	12	11.2	0.484	2.529	**
P. innesi, Lago Yahuacaca	20	10	11	11.0	0.224		
P. innesi, Lago Yahuacaca	20	10	11	11.0	0.224	11.221	**
P. axelrodi, Tapurucuara	36	11	13	12.3	0.535		
P. innesi, Lago Yahuacaca	20	10	11	11.0	0.224	13.893	**
P. axelrodi, Rio Morocoto	13	12	14	12.8	0.555		
P. innesi, Lago Yahuacaca	20	10	11	11.0	0.224	11.608	**
P. axelrodi, Cño Muco	18	12	14	12.6	0.608		
P. axelrodi, Tapurucuara	36	11	13	12.3	0.535	1.700	**
P. axelrodi, Caño Muco	18	12	14	12.6	0.608		
P. axelrodi, Tapurucuara	36	11	13	12.3	0.535	2.914	**
P. axelrodi, Rio Morocoto	13	12	14	12.8	0.555		
P. axelrodi, Caño Muco	18	12	14	12.6	0.608	1.103	NS
P. axelrodi, Rio Morocoto	13	12	14	12.8	0.555		

† Square-root transformations were used in computing the value of t. Two-tailed test; * indicates $P < 0.05$; ** indicates $P < 0.01$; NS (not significant) indicates $P > 0.05$.

P. simulans are based mostly on juveniles and on adults raised in an aquarium. Because of possible growth aberrancy we only suggest that these differences should be investigated in the future with wild caught and preserved samples.

The above data and those presented in the key indicate that *P. axelrodi* and *P. innesi* share more characters with each other than either one or the other shares with *P. simulans*. However, it does not necessarily follow that *P. axelrodi* and *P. innesi* are sister taxa because many of the characters they share may be primitive. We were unable to establish the polarity of many of the traits since we have no precise outgroup hypothesis. An example is the orbital bones of the neon tetras (Fig. 28). The orbital series of both *P. axelrodi* (Fig. 28A) and *P. innesi* (Fig. 28B) includes a large third infraorbiral, a similarity. However, this is probably a primitive character for *Paracheirodon*, present in the ancestor of all three neon tetras. The loss of the bone in *P. simulans* may therefore represent an autapomorphy. Since autapomorphies and plesiomorphies are not informative about relationships, the similarity of the presence of the third orbital in *P. axelrodi* and *P. innesi* probably tells nothing about relationships among the three species. Likewise, other characters such as laterosensory canal reduction, fin length, body proportions, fin-ray numbers, and others cannot be used because we were unable to evaluate their polarity. We thus have been unable to determine confidently the relationships among the species of *Paracheirodon*.

There is one character which appears unique to *P. axelrodi* and *P. innesi* within the characiforms. In life these two species

Table 6. Similarities and differences among perforated lateral-line scale counts of population samples of three species of *Paracheirodon*.†

	n	Range		$\bar{X}$	SD	*t*	*P*
Comparison between:							
P. simulans, Puerto Correño	20	0	5	2.6	1.569	8.717	**
P. axelrodi, Tapurucuara	26	5	8	6.5	0.762		
P. simulans, Puerto Correño	20	0	5	2.6	1.569	4.186	**
P. axelrodi, Rio Morocoto	7	5	7	6.0	0.577		
P. simulans, Puerto Correño	20	0	5	2.6	1.569	—	—
P. axelrodi, Caño Muco	1	6	6	6.0	—		
P. simulans, Puerto Correño	20	0	5	2.6	1.569	4.451	**
P. innesi, Lago Yahuacaca	20	3	6	4.6	0.940		
P. innesi, Lago Yahuacaca	20	3	6	4.6	0.940	7.333	**
P. axelrodi, Tapurucuara	26	5	8	6.5	0.762		
P. innesi, Lago Yahuacaca	20	3	6	4.6	0.940	3.424	**
P. axelrodi, Rio Morocoto	7	5	7	6.0	0.577		
P. innesi, Lago Yahuacaca	20	3	6	4.6	0.940	—	—
P. axelrodi, Caño Muco	1	6	6	6.0	—		
P. axelrodi, Tapurucuara	26	5	8	6.5	0.762	—	—
P. axelrodi, Caño Muco	1	6	6	6.0	—		
P. axelrodi, Tapurucuara	26	5	8	6.5	0.762	1.592	NS
P. axelrodi, Rio Morocoto	7	5	7	6.0	0.577		
P. axelrodi, Caño Muco	1	6	6	6.0	—	—	—
P. axelrodi, Rio Morocoto	7	5	7	6.0	0.577		

† Square-root transformations were used in computing the value of *t*. Two-tailed test; * indicates $P < 0.05$; ** indicates $P < 0.01$; NS (not significant) indicates $P > 0.05$.

have the blue lateral body stripe somewhat dorsal in position and terminating posteriorly in the vicinity of the adipose fin, rather than reaching the caudal-fin base as in *P. simulans*. In all other characids known to us the body stripe, when present, continues to the caudal-fin base. This character is unique to these species and therefore may represent a synapomorphy relating them.

Another character which may represent a synapomorphy for *P. axelrodi* and *P. innesi* is a short, or at least blunt, ascending premaxillary process (compare Figs. 19–23), as reported by Géry (1960b: 9, footnote). However, as reported by Géry and confirmed by us, several species of *Cheirodon* also have a short or blunt ascending premaxillary process. Our own personal bias is that the situation is convergent and that *Cheirodon* and *Paracheirodon* acquired this character independently, making it a synapomorphy for *P. axelrodi* and *P. innesi*. However, this view cannot be maintained until a more precise outgroup hypothesis is available.

We have been able to find only one character unique to *P. axelrodi* and *P. innesi*, slender evidence that they are sister taxa relative to *P. simulans*. We suggest that this problem should be the subject of future investigation.

SUMMARY

1) The systematics of the American Characidae are reviewed, and it is stated that phylogenetic analyses of the family eventually will produce considerable alteration in our understanding of the interrelationships of its member taxa and of their classification.

TABLE 7. SIMILARITIES AND DIFFERENCES AMONG BRANCHED ANAL-FIN RAY COUNTS OF POPULATION SAMPLES OF THREE SPECIES OF *Paracheirodon*.†

	n	Range		$\bar{X}$	SD	t	P
Comparison between:							
P. simulans, Puerto Correño	25	15	18	16.0	0.707	0.131	NS
P. axelrodi, Tapurucuara	48	15	19	16.0	0.841		
P. simulans, Puerto Correño	25	15	18	16.0	0.707	0.000	NS
P. axelrodi, Rio Morocoto	13	14	17	16.0	0.707		
P. simulans, Puerto Correño	25	15	18	16.0	0.707	0.813	NS
P. axelrodi, Caño Muco	18	15	17	16.2	0.618		
P. simulans, Puerto Correño	25	15	18	16.0	0.707	6.340	**
P. innesi, Lago Yahuacaca	20	16	19	17.5	0.889		
P. innesi, Lago Yahuacaca	20	16	19	17.5	0.889	3.835	**
P. axelrodi, Tapurucuara	48	15	19	16.6	0.841		
P. innesi, Lago Yahuacaca	20	16	19	17.5	0.889	5.137	**
P. axelrodi, Rio Morocoto	13	14	17	16.0	0.707		
P. innesi, Lago Yahuacaca	20	16	19	17.5	0.889	5.339	**
P. axelrodi, Caño Muco	18	15	17	16.2	0.618		
P. axelrodi, Tapurucuara	48	15	19	16.6	0.841	2.093	*
P. axelrodi, Caño Muco	18	15	17	16.2	0.618		
P. axelrodi, Tapurucuara	48	15	19	16.6	0.841	2.450	**
P. axelrodi, Rio Morocoto	13	14	17	16.0	0.707		
P. axelrodi, Caño Muco	18	15	17	16.2	0.618	0.698	NS
P. axelrodi, Rio Morocoto	13	14	17	16.0	0.707		

† Square-root transformations were used in computing the value of t. Two-tailed test; * indicates $P < 0.05$; ** indicates $P < 0.01$; NS (not significant) indicates $P > 0.05$.

2) The relationships and classification of the three known neon tetras, *Paracheirodon*, are reviewed and chosen as an example of the kinds of phylogenetic problems that will arise in the phylogenetic study of American characids.

3) The monophyly of *Paracheirodon* is documented by eight synapomorphic characters, including two aspects of live color pattern (presence of intense blue or blue-green lateral body stripe and dense red pigment restricted to region ventral to lateral stripe), preserved color pattern (brown or black chromatophores underlying and extending dorsal to lateral stripe), the dorsally placed attachment of the pterotic aponeurosis to the skull, a dorsal position of the posttemporal-supracleithrum joint, the dorsal position of the epioccipital bridge on the skull, the attachment of the ventral posttemporal ligament to the intercalar on the lateral surface of the pterotic bone, and the sharply dorsally turned supraoccipital profile combined with a slender body form.

4) Characters of dental morphology, laterosensory system, and karyology are discussed and, with our current understanding of characid phylogenetics, found to be uninformative about relationships of the species of *Paracheirodon*.

5) The three species of *Paracheirodon*, *P. simulans*, *P. axelrodi*, and *P. innesi* are diagnosed and differentiated.

6) The evidence for interrelationships of the species of *Paracheirodon* is discussed and one character, the dorsal placement of the lateral blue body stripe in life and its posterior termination near the base of the adipose fin, is found to be unique to two, *P. axelrodi* and *P. innesi*. We were unable to hypothesize polarities

for other characters common to any pair of the three species because all of the characters appear in at least some other possibly related taxa and because we were unable to hypothesize a precise outgroup.

ACKNOWLEDGMENTS

The following persons and institutions have aided this work in a variety of ways. Paulo Vanzolini, Director of MZUSP, allowed us to survey the collections in his charge and the Fundação de Amparo à Pesquisa do Estado de São Paulo supported collection of specimens by the EPA under Vanzolini's direction. Financial support for examining specimens at MZUSP and for collecting specimens in the Amazon basin was provided by the Smithsonian Institution Neotropical Lowland Research Program directed by Clifford Evans and later by Ronald Heyer. A National Geographic Society grant to the senior author was provided for collecting in Brazil and Venezuela. A. W. Crompton and Karel F. Liem provided space and facilities for research on the project while the senior author was a Visiting Alexander Agassiz Curator at the MCZ. Heraldo Britski and Naercio Menezes, MZUSP, provided aid in locating specimens and locality information on specimens in their care as well as loaning and exchanging important specimens. Warwick E. Kerr and Eneas Salati, consecutive directors of INPA, made available the facilities of that institution. Michael Goulding (INPA), Marilyn Weitzman, and Alfonzo Doas aided the authors' field work in the Amazon basin. A grant to Michael Goulding from the World Wildlife Fund, U.S., Washington, D.C. aided the field work. Francisco Mago-Leccia of MBUCV loaned and exchanged specimens in his care. Jamie Thomerson, Southern Illinois University, and Ross Socolof provided specimens collected in Colombia. Robert K. Johnson and Donald Stewart, FMNH; James E. Böhlke and William Saul, ANSP; and William Eschmeyer and Pearl Sonoda, CAS, loaned specimens for study.

Sara Fink prepared Figures 4 and 21 to 27, and portions of Figures 6 to 20. Marilyn Weitzman labeled the figures. Both Marilyn Weitzman and Sara Fink aided with sorting specimens at MZUSP and in record keeping; both read the manuscript and offered numerous suggestions. Sven Kullander, Antonio Machado, Francisco Mago-Leccia, Naercio Menezes, James Tyler, and Richard Vari read parts of the manuscript and provided advice and suggestions. Marilyn Weitzman, Christine Fox, Patricia Whorl, and Jean Smith typed various parts of the manuscript. Kurt Bruwelheide, Edgar N. Gramblin, Karsten E. Hartel, Robert Kanazawa, Lynn Pilkonis, and George Van Dyke provided technical assistance.

Publication costs of this study were covered in part by a grant from the Wetmore Colles Fund.

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APPENDIX 1, SPECIMENS EXAMINED

The characid specimens in the following list formed the basis for the comparative comments and for outgroup comparisons. In nearly all cases it was possible to examine alizarin preparations. Additional alizarin preparations listed in Weitzman (1962) belong to the following species: *Aphyocharax alburnus* (Günther), *Astyanax fasciatus mexicanus* Filippi, *Brycon meeki* Eigenmann and Hildebrand, *Bryconamericus brevirostris* (Günther), *Bryconamericus ortholepis* Eigenmann, *Grundulus bogotensis* (Humboldt and Valenciennes), *Hemigrammus nanus* Lütken, *Hemigrammus unilineatus* Gill, and *Tetragonopterus argenteus* Cuvier. Three species of *Cheirodon*, listed in Fink and Weitzman (1974), were examined, *C. affinis* (Meek and Hildebrand), *C. dialepturus* Fink and Weitzman, and *C. terrabae* Bussing.

There were species in some genera, e.g., *Tyttobrycon* Géry, which we were not able to examine. Comparison of these with *Paracheirodon* awaits new collections and further studies. Many other species in the genera listed below or in other genera were examined, mostly from specimens that were not alizarin preparations. Those listed below were selected to be examined in detail for a variety of reasons. Most are morphologically representative of the genera to which they have been assigned by past authors.

Aphyodite sp.—2 alizarin preparations, SL 22.1–11.7 mm, USNM 221932, Brazil, Amazonas, Lago Hyanuary (=Janauarí) (30°13'S, 60°9'W), near Manaus, Thayer Expedition, Major Coutinho, November–December 1865. [Dick, 1977, Figure 10 shows Lago Hyanuary (now spelled Janauarí) to be along the northeastern side of the Rio Negro northwest of Manaus. Lago Janauari lies south of Manaus on the neck of land between the confluence of the Rio Negro and the Rio Solimões. Mrs. Agassiz (Agassiz and Agassiz, 1868: 253) states that the lake is on the west side of the Rio Negro. Currently a lake with this name lies on the opposite side of the Rio Negro from Manaus, to the southwest.]

Astyanax fasciatus mexicanus (Filippi).—3 alizarin preparations, SL 37.5–60.3 mm, from 19 spms, MCZ 41365, Mexico, Tamaulipas, Río Guayalejo (approximately 23°0'N, 98°50'W), W. A. McLane and N. Marshall, December 1939.

Axelrodia riesei Géry.—6 alizarin preparations, SL 15.2–17.6 mm, USNM 221681, from 20 spms, USNM 231821, Colombia, Vaupés, Río Vaupés at Mitú (1°7'N, 70°4'W), H. R. Axelrod, November 1964.

Brittanichthys axelrodi Géry.—2 alizarin preparations, SL 19.8–22.2 mm, USNM 221682, Colombia, Vichada, Río Orinoco basin, Río Muco 50 km west of San Jose de Ocune (4°14'N, 70°50'W), R. Socolof, 3–5 July 1974.—17 alizarin preparations, SL 15.3–24.1 mm, USNM 221992, from 60 spms, USNM 221991 (also 60 spms at MZSUP), Brazil, Amazonas, Rio Negro drainage, near mouth of Rio Urubaxi (0°24'S, 65°2'W), M. Goulding, 11 February 1980.

Bryconamericus meridae (Eigenmann).—4 alizarin preparations, SL 25.9–39.2 mm, USNM 221933, from 193 spms, USNM 121469, Venezuela, Trujillo, Maracaibo basin, Río Motatán, 4 km above Motatán (9°19'N, 70°35'W), L. P. Schultz, G. Zuloaga, W. H. Phelps Jr., 15 March 1942.

Bryconella pallidifrons (Fowler).—1 holotype of *Cheirodon pallidifrons* Fowler, SL 22.8 mm, ANSP 71728, aquarium spm donated 3 July 1940 by J. L. Troemner.—1 holotype of *Hyphesssobrycon thompsoni* Fowler, SL 18.4 mm, ANSP 71849, aquarium spms donated March 1949 by H. E. Thompson.—6 spms, SL 21.4–27.4 mm, USNM 216205, aquarium spms imported with *Paracheirodon innesi*, 1976, probably from near Leticia, Colombia.—4 alizarin preparations, SL 19.0–27.4 mm, USNM 221676, same data as USNM 216205.—5 spms, SL 18.8–20.7 mm, MCZ 52163, Colombia, Amazonas, Río Marañon, several km upriver from Leticia, small stream flowing into Lago Yahuacaca (4°6'S, 69°58'W), W. L. Fink, 3 December 1976.—2 spms, SL 18.2–18.5 mm, USNM 216701, same data as MCZ 52163.

Characidium sp.—2 alizarin preparations, SL 27.8–35.5 mm, USNM 222017, from 68 spms, USNM 222017, Colombia, Vichada, Río Orinoco basin, Caño Muco, 50 km west of San Jose de Ocune (4°14'N, 70°50'W), R. Socolof, 3–5 July 1974.

Cheirodon australe Eigenmann.—2 alizarin preparations, SL 32.1–46.4 mm, USNM 221998, from 14 paratypes, USNM 84317, Chile, Llanquihue, creek flowing into Lago Llanquihue at Puerto Varas (41°20'S, 72°68'W), C. H. Eigenmann, 12 March 1919.

Cheirodon galusdae Eigenmann.—2 alizarin preparations, SL 30.6–52.1 mm, USNM 221997, from 11 paratypes, USNM 84319, Chile, Talca, Río Loncomilla (=Río Locomilla of Eigenmann) at San Javier (=San Xavier of Eigenmann) (35°35′S, 71°44′W), C. H. Eigenmann, 23 March 1919.

Cheirodon interruptus (Jenyns).—16 alizarin preparations, SL 14.0–33.9 mm, USNM 221674, from 107 spms, USNM 221673 (an equal number of spms at MZUSP), Brazil, Rio Grande do Sul, Município de Rio Grande, Arroio Senandes where it crosses road between Rio Grande and Cassino (32°09′S, 52°11′W), N. Menezes, L. Chao, S. Weitzman, M. Weitzman, and L. Jardim, 10 December 1979.—3 alizarin preparations, SL 19.8–40.6 mm, from 36 spms, FMNH 50629, Uruguay, Minas, Arroyo Polanco (33°56′S, 55°20′W), tributary to Río Cebollati, C. C. Sanborn, December 1926.

Cheirodon piaba Lütken.—3 alizarin preparations, SL 18.0–22.7 mm, from 17 spms, FMNH 50136, Brazil, Paraná, Rio Itararé (24°7′S, 49°20′W) a town on Rio Itararé, tributary to Rio Paranapanema, E. R. Blake, September 1937.

Cheirodon pisciculus Girard.—1 alizarin preparation, SL 52.3 mm, USNM 221996, from 9 spms, USNM 84316, Chile, Valparaiso, Río Aconcagua at La Calera (32°47′S, 71°12′W), C. H. Eigenmann, 13 April 1919.—2 alizarin preparations, SL 39.2–41.5 mm, from many spms, CAS 20655 (IUM 15504), Chile, Santiago, Río Maipo basin Río Angustura at Hospital (33°52′S, 70°55′W), C. H. Eigenmann, 22 April 1919.—1 alizarin preparation, SL 28.6 mm, USNM 222009, from 9 spms, USNM 84318, same locality data as CAS 20655.

Elachocharax geryi Weitzman and Kanazawa.—1 alizarin preparation, SL 12.5 mm, USNM 215288, Colombia, Vichada, Río Orinoco basin, Caño Muco (between 4°14′N, 70°2′W and 4°58′N, 71°58′W), a tributary to Río Vichada, J. E. Thomerson, D. L. Hicks, and J. H. Vaques, 24 April 1974.

Gymnocorymbus thayeri Eigenmann.—1 alizarin preparation, SL 27.5 mm, CAS(IUM) 15881, Peru, Loreto, brooks and ponds at Iquitos (3°45′S, 73°12′W), W. R. Allen, September 1920.

Hemigrammus erythrozonus Durbin.—1 lectotype, SL 23.4 mm, FMNH 53546, Guyana (=British Guiana), Essequibo, Erukin Creek (5°18′N, 59°16′W), lower Potaro River, C. H. Eigenmann, 30 October 1908.—5 spms, "paralectotypes," SL 21.1–23.3 mm, CAS(IUM) 11905, same data as FMNH 53546.—5 alizarin preparations, SL 22.9–32.5 mm, USNM 216709, aquarium spms, December 1976.

Hemigrammus levis Durbin.—4 alizarin preparations, SL 17.0–41.6 mm, USNM 221938, from 28 spms, USNM 221937, Brazil, Amazonas, Rio Negro basin, Rio Jufari (=Rio Tupari), between Santa Fe and Castanheiro Grande (mouth of Rio Jufari is at 1°23′S, 62°0′W), M. Brittan, 21 April 1964.

Hemigrammus pulcher Ladiges.—3 alizarin preparations, SL 19.0–23.1 mm, USNM 221936, Colombia, Amazonas, Leticia (4°13′S, 69°56′W), D. Kramer, 4 December 1974.

Hemigrammus rhodostomus Ahl.—1 alizarin preparation, SL 29.1 mm, USNM 222018, from 5 spms, USNM 94305, Brazil, Pará, Ilha de Arapiranga (no specific site designated), 1934. These specimens were discussed by Myers in Eigenmann and Myers (1929: 352).

Hemigrammus sp.—16 alizarin preparations, SL 13.6–30.4 mm, USNM 221671, from 99 spms, USNM 221672, Brazil, Pará, Rio Marituba at Marituba (1°25′S, 48°15′W), B. B. Collette, 23 May 1975.

Hyphessobrycon compressus (Meek).—1 alizarin preparation, SL 30.7 mm, USNM 204387, from 3 spms, FMNH 4642, Mexico, Oaxaca, El Hule, S. E. Meek, 22 April 1903.

Hyphessobrycon sp.—18 alizarin preparations, SL 13.1–25.9 mm, USNM 221679, from 147 spms, USNM 221680, Brazil, Pará, Rio Ihangapi at Ihangapi (0°9′S, 47°9′W), B. B. Collette, 23 May 1975.

Hyphessobrycon loretoensis Ladiges.—8 alizarin preparations, SL 13.9–20.3 mm, USNM 221675, from 42 spms, USNM 216700, Colombia, Amazonas, Rio Loreto-Yacu (3°30′S, 70°10′W), N. Navarro C., November 1976.

Hyphessobrycon lütkeni (Boulenger).—15 alizarin preparations, SL 11.9–37.1 mm, USNM 221677, from 204 spms, USNM 221678 (an equal number of spms at MZUSP), Brazil, Rio Grande do Sul, southeast of Pôrto Alegre, Município de Viamão, small tributary of Rio Fiuza along Paso Comprido, N. Menezes, S. Weitzman, and M. Weitzman, 9 December 1979.

Klausewitzia aphanes Weitzman and Kanazawa.—2 alizarin preparations, SL 14.8–14.9 mm, USNM 221995, from 14 spms, USNM 213783, aquarium spms imported with *Paracheirodon axelrodi* from Manaus, Brazil, probably collected during 1975 from "upper Rio Negro."

Leptobrycon sp.—1 alizarin preparation, SL 21.7 mm, USNM 222013, from 4 spms, USNM 222012, Venezuela, Amazonas, Río Atabapo (4°3′N, 67°43′W), tributary to Rio Orinoco, A. Cortez, J. O. Silva, 23 February 1974

Microschemobrycon casiquiare Böhlke.—2 alizarin preparations, SL 25.1–25.3 mm, from 29 spms, CAS(SU) 17511, paratypes, Brazil, Amazonas, Rio Negro at Cucuy (=Cucuhy) (1°12′N, 66°50′W), C. Ternetz, 14 February 1925.

Microschemobrycon sp.—8 alizarin preparations, SL 25.1–30.8 mm, USNM 221911, from 33 spms, USNM 221912 (25 spms at MZUSP), Brazil, Amazonas, Rio Aripuanã, tributary of Rio Madeira (5°8′S, 60°24′W), H. Britski, N. Menezes, 7 November 1976.

Neolebias olbrechtsi (Poll).—2 alizarin preparations, SL 22.0–23.8 mm, USNM 222015, Zaire, stream flowing into Lake Tumba near Bikoro, collector and date unknown.

Oxybrycon sp.—1 alizarin preparation, SL 14.1 mm, CAS(SU) 47192, Brazil, Amazonas, Rio Negro at Cucuy (=Cucuhy) (1°12′N, 66°50′W), C. Ternetz, 14 February 1925.

Parecbasis cyclolepis Eigenmann.—1 spm, SL 53.5 mm, ANSP 144104, Peru, Maynas, vicinity of Iquitos

(3°45′S, 73°12′W), Rio Nanay, Catherwood Expedition, 14 October 1945.

Pristella sp.—2 alizarin preparations, SL 28.9–33.8 mm, USNM 222008, from 6 spms, USNM 66267, Guyana (=British Guiana), trenches, Botanic Gardens at Georgetown (6°47′N, 58°10′W), S. E. Shidler, September 1908,—2 alizarin preparations, SL 17.2–22.1 mm, USNM 222011, from 6 spms, USNM 222010, Surinam, Pará, 43 km south of Paramaribo, blackwater creek near islands, Bosbeheer HQ at Zanderij, D. W. Dunham, 9 April 1969.

Thrissobrycon pectinifer Böhlke.—1 alizarin preparation, paratype, SL 24.0 mm, CAS(SU) 16945, Colombia, Vaupés, Rio Negro, "from a sand bank on the Colombian border," C. Ternetz, 14 February 1925.

Tyttocharax madeirae Fowler.—6 alizarin preparations, SL 13.5–17.9 mm, USNM 222007, from 52 spms, USNM 179540, Brazil, Amazonas, Rio Urubú, "about 25 km from Itacoatiara (3°7′S, 58°39′W), H. Schultz, October 1958.

APPENDIX 2, TYPE LOCALITIES OF SPECIES OF *PARACHEIRODON*

All of the neon tetras, as originally described, were accompanied by erroneous or vague locality information. The following account is offered to bring the record up-to-date.

Myers (1936: 97) listed the type locality of *P. innesi* as follows. "It formed part of an importation obtained by a French collector of aquarium fishes from the Peruvian Amazon; it was received by Mr. Innes directly from the importer in Paris for identification, together with information making it seem likely that the locality was near Iquitos." Subsequently Innes (1936) published an account of the introduction of *P. innesi* into the aquarium trade, making it clear that the holotype (USNM 102109) is a specimen from the original importation sent to Paris in 1936 from South America. Stoye (1936) published an article about the discovery of *P. innesi* based on an interview with August Rabaut, the collector. The fishes were taken in March and/or April 1936 during a trip by canoe traveling up the Rio Putumayo into the State of Amazonas, Colombia. The precise locality in this region is not recorded and the specimens may have been obtained from several localities. Since then many millions of neon tetras have been exported from the areas of Peru and Colombia adjacent to the Rio Putumayo and from areas in Peru, Colombia, and Brazil adjacent to Tabatinga and Leticia. Ladiges (1973, 1978, and 1979) provided information on the discovery of *P. innesi*. Geisler (1979) published an account of collecting *P. innesi* in the Rio Curaray, a tributary of the Rio Napo in Peru.

It was not until 1960 that specimens with exact locality data found their way into the scientific community (Géry, 1965a: 31). These specimens were from the Igarapé Prêto near the little village of Belém, Amazonas, Brazil, about 60 km downstream on the Rio Solimões from the border region between Brazil, Colombia, and Peru. The only other specimens with locality data known to us are those reported here.

The history of the discovery of *P. axelrodi* is more complex than that of *P. innesi* or *P. simulans*, but its distribution now seems clear. *Paracheirodon axelrodi* was described nearly simultaneously by Schultz (1956) and by Myers and Weitzman (1956). These two sets of authors recorded different type localities. Schultz (1956: 42) reported his two specimens as being from somewhere near Pôrto Velho [on the Rio Madeira], Amazonas, Brazil. At the end of Schultz's description (p. 43) the editor appended a short note that the specimens used in the description were supplied by H. R. Axelrod who obtained them from Sol Kessler of the Fish Bowl, New Jersey. Axelrod (1956: 16) reported that this species was brought to his attention on February tenth or eleventh by several of his friends and that specimens received from Mr. Kessler were the ones sent to Schultz at the Smithsonian Institution for identification. Axelrod (1956: 17) further reported that he was unable to get information on the collecting locality of *P. axelrodi* from the importers, Fred Cochu and Mr. Schnelle of Paramount Aquarium Inc., but that the locality information he did get came from a person (unnamed) who formerly collected fishes in the region where these fishes are found. Axelrod (1956: 17) stated that this person told him that this species came from north of Pôrto Velho on the Rio Madeira.

Myers and Weitzman (1956: 1) gave as their type locality for *Hyphessobrycon cardinalis* (=*P. axelrodi*), "Rio Negro, Amazonas, Brazil." They reported receiving their specimens and locality information from Paramount Aquarium Inc. through W. T. Innes. They recorded more complete information on the label in the bottles (SU 48710, holotype, and SU 48711, eleven paratypes and SU 48712, 2 alizarin specimens, all now at CAS) as Tomar (0°25′S, 63°55′W) on the Rio Negro, State of Amazonas, Brazil, collected in the winter of 1955–1956. This more precise information was supplied by Paramount Aquarium Inc., but its publication was withheld at their request. Weitzman (1956: 257–258) provided some history of the discovery of *P. axelrodi*, citing Ladiges (1956) as a source. Weitzman noted that this fish is from the Rio Negro, not the Rio Madeira and that Ladiges (1956) stated that in 1953 he received a letter from Prof. Harold Sioli, a well known German limnologist studying the river systems of the Amazon basin, stating that in September of 1952 he (Sioli) found a neon tetra near the mouth of the Rio Uaupes (=Vaupés in Colombia) and the Rio Içana near São Felipe. Both streams are tributaries from the west to the Rio Negro with their headwaters in Colombia.

In February of 1979 one of us (Weitzman) discussed this discovery with Professor Sioli who later provided the following information derived from his field notes for 1952. "In the fall of 1952 I made a trip to the upper Rio Negro together with some colleagues of the Instituto Agronomico do Norte, Belém and Prof. Theodosius Dobzhansky. On September 24, 1952 I collected hydrobiological material in front (river side) of Içana (formerly São Felipe) near Sitio Caburis. I looked into a very small forest pond, less than one meter wide and deep, and among the dead leaves on the bottom I suddenly saw in the brown water some silvery double-points [eyes with silvery pigment over their dorsal surface]. I quickly dipped my net into the water and caught some beautiful-coloured fishes, red and blue, which I, as a non-ichthyologist, thought to be the neon tetra, *Hyphessobrycon innesi*. I only wondered to find that species so far distant from the area around Leticia on the upper Solimões river, from where the fish is commonly exported for aquarium hobbyists." Prof. Sioli preserved and labeled a few specimens with locality information and later (1953) sent them to Dr. Ladiges, then at the Zoological Institute of the University of Hamburg. Apparently the fish were lost in the mail, for Ladiges never received the specimens. Prof. Sioli also noted that he mentioned this discovery to Dietrich Horie of Belém, who at that time organized the fishing expeditions for Mr. Cochu of Paramount Aquarium Inc., New York.

In retrospect, it might now appear that Prof. Sioli could have collected either *P. axelrodi* or *P. simulans*; however, one of us (Weitzman) interviewed the aquarium fish collector and exporter H. Willi Schwartz of Manaus, Brazil in 1977 concerning the habitats and collecting sites of *P. axelrodi* and *P. simulans*. The two species appear to have the same or at least partly the same geographical range. Mr. Schwartz reported that *P. axelrodi* is ordinarily found in the lower portions of the streams tributary to the upper Rio Negro, while *P. simulans* occurs upstream and rarely, if ever, are the two species found at the same location. This would make it seem very probable that Sioli actually captured *P. axelrodi* since he captured his specimens near the Rio Negro.

Axelrod (1976 and 1980) has published accounts of the discovery of *P. axelrodi* differing from that reported above.

Paracheirodon simulans was described by Géry (1963) and the types were stated to have been collected by H. W. Schwartz from the Rio Purus during November of 1962. Géry (1966c: 231) corrected this locality to the Rio Jufaris (or Tupari), which empties into the Rio Negro near the mouth of the Rio Branco. The correction was supplied to Géry by the collector, H. W. Schwartz.

Citing aquarium collectors as his source, Géry (1966c: 231–232) discussed the distribution of the neon tetras. The records we include above considerably expand the locality information provided by Géry for *P. axelrodi* and especially for *P. simulans*. Géry (1966c: 232) stated that *P. innesi* is present along the Rio Solimões from São Paulo de Olivença in Brazil and along the Rio Marañon (the name for the Rio Solimões in Peru) up to Iquitos in Peru. We have no information for the existence of *P. innesi* in that region of the Rio Marañon but have no reason to doubt this possibility. Kullander's report, noted here under the species description of *P. innesi*, of specimens from the lower Rio Ucayali in Peru would seem to confirm Géry's report and to extend the range somewhat.

APPENDIX 3, COMMENTS ON CHARACTERS CURRENTLY PHYLOGENETICALLY UNINFORMATIVE

Three character systems, the dental morphology, the laterosensory system, and karyology commonly vary in characids and, at least in the first two, are easily accessible for morphological and systematic investigation. These have been used frequently in the past to assess relationships among characids. As explained below, we have serious doubts about the current use of these characters. We are certain that these characters are phylogenetically significant at some of the various taxonomic levels in the characids that have them. At other levels they probably represent homoplasies. We have been unable to evaluate their phylogenetic appropriateness for *Paracheirodon*. This is because of the widespread but sporadic occurrence of these characters in many characids and because of our failure to find specific outgroups for *Paracheirodon*. It is our view that caution is necessary in utilizing the characters discussed below. One should not propose hypotheses of relationship beyond the limits of homology (synapomorphy) established by a combination of the study of morphological similarity, the application of outgroup comparison, and the determination of a parsimonious distribution of characters among the studied taxa. Our viewpoint about the use of ontogeny in the assessment of character polarity is discussed by Fink (1982).

Since these characters have been applied by others, as explained below, to questions of relationship about the species we place in *Paracheirodon*, we find it useful to discuss them at this point.

Dental Morphology. This character "complex" historically has been one of the most important in characid classification. Numbers of tooth rows on the premaxillae define "subfamilies," e.g.: two tooth rows, Tetragonopterinae, Eigenmann (1917: 38–43); one row, Cheirodontinae, Eigenmann (1915: 3–10). In combination with other characters, numbers of teeth in the premaxillary rows define genera. For example, there are five inner row premaxillary teeth in *Astyanax* and four teeth in *Bryconamericus*. Consideration of relationships based on interpretations of tooth morphology has been the primary source of the "neon tetra problem." In the absence of synapomorphies diagnostic of *Paracheirodon*, *P. axelrodi* and *P. innesi* would be "cheirodontine" (in different genera) and *P. simulans* "tetragonopterine." Our assessment that these three species form a monophyletic group forces a reconsideration of dental morphology, specifically as applied to the problem of interrelationships within *Paracheirodon*. Unfortunately, our lack of a precise hypothesis of outgroups prevents us from utilizing such similarities as are present in the group. For example, *P. simulans* (Fig. 19A–D) has two rows of premaxillary teeth while *P. axelrodi* (Fig. 20A–D) and *P. in-*

nesi (Fig. 21A-D) have one row. If we find that there are two rows in the outgroup, the single row would be synapomorphous for the *axelrodi-innesi* pair. If, on the other hand, there is a single row in the outgroup, the two rows of *P. simulans* is an autapomorphy. Likewise, the analysis of tooth-cusp number: adult *P. simulans* have six to nine cusps on the large jaw teeth, adult *P. axelrodi*, five to seven, and adult *P. innesi*, three. Two alternative subgroups are possible, one based on cusp reduction (*P. axelrodi-P. innesi*), and the other on a cusp increase (*P. axelrodi-P. simulans*). Again, lack of an appropriate outgroup prevents use of these similarities.

We must admit that our personal biases suggest that the single tooth row and reduced cusp number are derived characters for *Paracheirodon*. The supposition regarding the former character is in part based on our observation (discussed in the Description Section) that *P. innesi* of advanced age occasionally develop a second tooth row (Fig. 23A–D). Nevertheless, our biases are unsupported by solid evidence and must be left out of the analysis.

Laterosensory System, Cranium, Pectoral Girdle, and Associated Structures. Laterosensory system reduction in *Paracheirodon* is extensive on both the head and body and formed part of the basis for the discussion of the relationships of *P. axelrodi* and *P. innesi* by Géry (1960b: 8–13). Laterosensory reductions in the postocular skull region were illustrated by Géry (1960b: 10–11, Figs. 6–8). In comparing his drawings with our cleared and stained specimens of these species we found a variety of discrepancies. Before proceeding with our own discussion of this region we find it appropriate to review Géry's efforts. Géry (1960b) noted that *P. innesi* and *P. axelrodi* have this region "comparable" (p. 9) and "the same" (p. 11). But on page 12 he stated: "Compared to *Cheirodon axelrodi* these structures [in *P. innesi*] (in particular the circumorbital and otic series) make believe [sic] that the two forms [*P. axelrodi* and *P. innesi*] which are also extremely similar, have evolved independently from a common cheirodontine ancestor and probably recently." This statement seems to indicate that Géry detected differences in this region which, along with those he found in the jaws, prompted him to hypothesize convergence of external characters such as color pattern for these two fishes. However, Géry's illustrations (Fig. 7) of the postocular skull of these two neon tetras show some rather drastic differences in the bones he labelled as epiotic, supratemporal, and posttemporal. Upon comparison of Géry's illustrations with the specimens at hand, we find a considerable amount of error in both his drawing and labeling. Compare Géry's illustrations with Figures 4, 5, 7 of *P. axelrodi* and 8 of *P. innesi* in the present paper and note their similarity to Figure 6 of *P. simulans*. In both of Géry's illustrations the bone labeled as the cleithrum is the supracleithrum and that labeled as the supracleithrum is the posttemporal. In both illustrations Géry divided the frontal into two parts, labeling the anterior part the frontal and the posterior part the parietal. In both drawings he illustrated a supraorbital, a bone we found absent in all our cleared and stained specimens of *P. axelrodi* and *P. innesi* and in all "tetragonopterine" characids examined. The epioccipital (=epiotic) is not illustrated in his drawings. In his drawing of *P. innesi* he divides the parietal into two parts, labeling one the epiotic and the other supratemporal. In his drawing of *P. axelrodi* he divides the pterotic into two bones, labeling one the supratemporal and the other the pterotic. The exoccipital, epioccipital (=epiotic), and basioccipital bones are not present in Géry's drawings. He labels the parietal as the epiotic. With these kinds of errors in morphological representation we can place little confidence in Géry's statements about relationships based on his observations.

Reductions of the laterosensory portions of the postocular cranium and shoulder girdle are as follows. Laterosensory canals are absent from all of the postocular cranial bones except the frontal (Figs. 4–8). The primitive laterosensory canal arrangement for characids is illustrated in Figures 9, 28A, 29 for *Astyanax* and Figures 10, 30 for *Gymnocorymbus.* Canal terminology used here follows Weitzman (1962: 65, Fig. 9). There are supratemporal and parietal canals in the parietal bone, a pterotic canal in the pterotic, all of which are absent in the species of *Paracheirodon* and, to varying degrees, in many small characids. *Cheirodon interruptus* (Fig. 11) shows relatively little laterosensory canal loss, whereas *Hemigrammus erythrozonus* (Fig. 12) shows considerably more. *Axelrodia riesei* (Fig. 13), *Brittanichthys axelrodi* (Fig. 14), and *Tyttocharax madeirae* (Fig. 15) have cranial laterosensory canal loss about equivalent to that of the neon tetras. The pygmy species of the Characidiinae, *Klausewitzia aphanes* (Fig. 17) and *Elachocharax geryi* (Fig. 18) also show much laterosensory canal loss.

The pterotic branch of the frontal laterosensory canal is absent in the neon tetras (Figs. 6–8). This branch is illustrated in its most extensive form in Figures 10, 30 of *Gymnocorymbus.* The canal is absent from the bone in *Astyanax* (Fig. 9) but is present in the skin over its surface (Fig. 29). The pterotic branch of the frontal canal is often reduced or lost in paedomorphic characids (Figs. 11–15, 18).

The neon tetras lack the extrascapular bone and its canal (Figs. 6–8). The primitive arrangement of the extrascapular bone with three openings and the laterosensory system is shown in Figures 9, 29 of *Astyanax* and Figures 10, 30 of *Gymnocorymbus.* The extrascapular is also absent in *Axelrodia* and *Brittanichthys* (Figs. 13, 14 respectively) and reduced in *Klausewitzia* (Fig. 17). In Figure 15 of *Tyttocharax* the small bone shown at the dorsal end of the supracleithrum is a posttemporal, not an extrascapular.

The posttemporal and supracleithrum are without laterosensory canals in the species of *Paracheirodon.* The primitive characid distribution of these canals is represented by *Astyanax* (Figs. 9, 29) and *Gymnocorymbus* (Figs. 10, 30). The canals are present in *Cheirodon interruptus* (Fig. 11) and *Hemigrammus erythrozonus* (Fig. 12), but absent in *Axelrodia riesei* (Fig. 13), *Brittanichthys axelrodi* (Fig. 14), and *Tyttocharax madeirae* (Fig. 15).

A suprapreopercular bone is absent in *Paracheirodon.* The bone is present in *Astyanax* (Fig. 9) and *Gymnocorymbus* (Fig. 10) as a tube bone dorsal to the preopercle and illustrated in the same pattern. The suprapreopercle is commonly absent in small characids (Figs. 11–18) and may be the first part of the head laterosensory system to be lost in small characids.

Other segments of the laterosensory system absent in *Paracheirodon* are the posterior infraorbitals and their canals of the circumorbital series (Fig. 24A–C).

The terminology we believe suitable for the circumorbitals was defined by Weitzman (1962: 28–31, Fig. 9). The term lachrymal, still extensively used in teleosts for the first (anterior) infraorbital, was excluded from consideration because there is no evidence of the homology of the bone with the lachrymal of non-teleostean vertebrates. Also, the terms "great suborbital" and "second suborbital," used for characids by Eigenmann in his extensive series of papers, is here called the third infraorbital. The bone is not a true suborbital as explained by Weitzman (1962: 28, footnote), and it is not the second bone in the infraorbital series. Terms such as suborbital and postorbital are used in several fossil fish groups for orbital bones which do not border the eye, and these orbital bones are not homologous with the infraorbital bones which do border the eye.

The antorbital is the most anterior element of the orbital series illustrated in Figures 4, 5, 28A,B. It lacks a laterosensory canal, lies in the posterolateral wall of the nasal capsule, and is dorsal to the first infraorbital.

The infraorbitals are numbered consec-

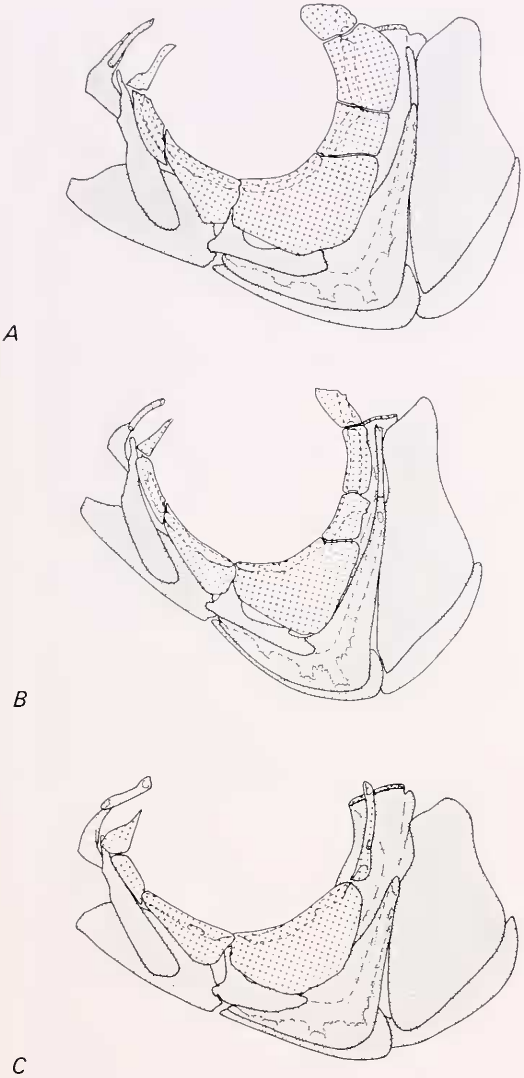

Figure 28. Face bones of three neotropical characids. Circumorbital bones represented by plus-sign (+) pattern. Lateral view, left side. A. *Astyanax fasciatus mexicanus*, SL 40.4 mm, MCZ 52104. B. *Gymnocorymbus thayeri*, SL 38.5 mm, MCZ 49962. C. *Hemigrammus erythrozonus*, SL 24.2 mm, USNM 216709.

Figure 29. Posterior region of skull and pectoral girdle of *Astyanax fasciatus mexicanus*, female, SL 52.4 mm, MCZ 41365, lateral view, left side. Distribution of laterosensory system illustrated by dense black dots.

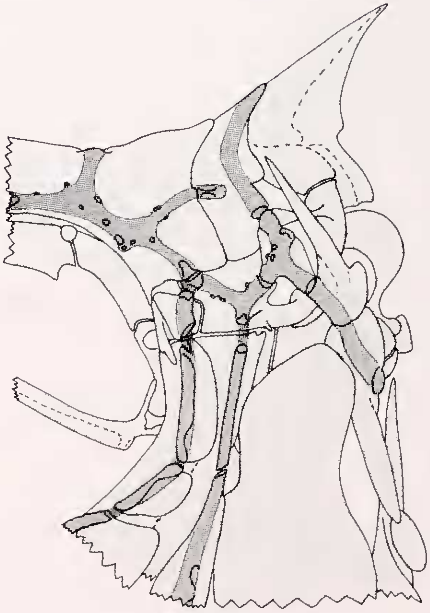

Figure 30. Postocular region of skull and pectoral girdle of *Gymnocorymbus thayeri*, adult, SL 27.5 mm, CAS(IUM) 15881, lateral view, left side. Distribution of laterosensory system illustrated by dense black dots.

utively, the anterior one being referred to as the first and the posterodorsal one as the sixth. The third infraorbital is the largest and apparently primitively has its ventral and posterior border along the preopercular laterosensory canal (Weitzman, 1960: 64, Fig. 8). In many characids the third infraorbital is reduced in size so that its distal border (that away from the eye) does not contact the border of the preopercular canal (Fig. 28A–C). All infraorbital bones have laterosensory canals in relatively primitive characids. The supraorbital is apparently absent in "tetragonopterine" characids but is present in *Brycon* and some other characids such as *Serrasalmus*.

Reductions or absence of infraorbital four, five, and six (Figs. 11–18, 28C), and reductions in perforated lateral-line scales are of common occurrence in small and medium sized characids. These characters, also found in *Paracheirodon*, have evolved repeatedly through paedomorphosis and may be labile, subject to being phenotypically reacquired through heterochrony. Such characters, although certainly phylogenetically significant at some level, in practice are difficult to use as synapomorphies. Although the laterosensory reductions present in the neon tetras may help define *Paracheirodon*, we find it impossible to use them until we have a precise hypothesis of outgroup relationships.

Karyology. A survey of the literature of fish systematics (and of many other groups) for the past two decades shows an increasing use of chromosome number and morphology as characters. We expect to see the use of chromosome data increase with the continued refinement and simplification of karyological methods. Chromosome features, like any other characters, must be subject to phylogenetic analysis. Phenetic similarity or simple possession of similar numbers of chromosomes or arms does not necessarily indicate close relationship. We know of very few attempts to interpret karyotypic data in fishes in the phylogenetic paradigm, at least at lower taxonomic levels (e.g., Wiley and Hall, 1975). Farris (1978) has discussed analysis of chromosomes in phylogenetic inference.

In the problem at hand, we find the available data flawed. Attempts to date to characterize the karyotypes of *P. axelrodi* and *P. innesi* have arrived at different results. For *P. axelrodi*, Post (1965: 65) found n = 24 while Scheel and Christensen (1970: 26) found n = 26. Post (1965) did not describe chromosome morphology, but Scheel and Christensen (1970: 31) state that the chromosomes include one pair with "short or very short secondary arms," with the rest "strictly one-armed" (see their figure on page 31). For *P. innesi* the latter authors (pp. 26, 31) give 2n = 32 as the chromosome number. They describe all as having "two arms," state that "twenty large two-armed elements represent derived elements produced by fusions of one-armed elements." Lueken and Foerster (1969: 172) report 2n = 36 for *P. innesi*, but our count from their Figure 3 is 2n = 32, which agrees with that of Scheel and Christensen. Scheel (1972: 62) gives the karyotype of *P. simulans* as n = 25 and 48 arms.

It is obvious that some disagreement about the karyotype of these fishes exists, and it is even more unfortunate that the above authors either presented their data without illustrations or in the form of photographs of crude cell squashes, with no presentation of serially arranged chromosomes, no indication of numbers of cells examined, no list of tissue examined, no locality data of examined specimens, and no voucher specimens deposited in museums. There is agreement among the authors that all three of the neon tetras have different karyotypes and we will present our discussion on the assumption that these differences are real.

Scheel and Christensen (1970: 31) and Scheel (1972: 65) attempted to use karyotypic data to determine whether the neon tetras are "closely related" and concluded that all are "distantly related," thereby implying that the three species should be kept in separate genera. Further, based on similarity of chromosome morphology and number, Scheel (1972: 65) considered the following characids to be closely related: *Hasemania marginata*, *Moenkhausia oligolepis*, *Thayeria boehlkei*, *Triportheus pictus*, *Hemigrammus caudovittatus*, *Hyphessobrycon bifasciatus*, *Nematobrycon palmeri*,[1] *Astyanax bimaculatus*, and *Gymnocorymbus ternetzi*. Scheel never explicitly defined the character he used to form this group, but our interpretation of his text is that the karyotype of each member has at least one, but up to five, large metacentric chromosomes. The only way to define the character as it was used is "presence of large metacentric chromosomes," disregarding the number of metacentrics. The logic of such a procedure escapes us. Nevertheless, in effect Scheel proposed a phylogenetic hypothesis greatly at variance with any current understanding of characid relationships. In spite of his statement that the karyotype shared by this assemblage could not possibly have developed independently, implying monophyletic relationship, we would hold that many characters in the morphology of these fishes would refute such a hypothesis, especially the putative "close relationships" of *Triportheus* and *Nematobrycon* with each other and with the other genera listed above. We suspect that sister group relationships will indeed be found between some species currently assigned to *Hemigrammus*, *Hyphessobrycon*, and *Hasemania*, but the evidence as presented and analyzed by Scheel is not suitable for the analysis. Instead, the data presented by Scheel (1972) indicate to us that gross chromosome morphology as studied by the above authors is quite labile in small characid species and that considerable comparative investigation of chromosome banding, with emphasis on the search for derived characters, will be needed before chromosome data will be useful in phylogenetic analysis of these fishes.

Based on data presented by the above authors, we note that each of the neon tetras has a karyotype different from the others, that both *P. simulans* and *P. axelrodi* have karyotypes which are similar to those of many other small characid species, and that *P. innesi* seems to have a unique, probably derived, karyotype. These data thus are not relevant to phylogenetic analysis since the characters are either primitive for characids or are autapomorphic.

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[1] Incorrectly placed in the Cheirodontinae.