Xenurobryconin Phylogeny and Putative Pheromone Pumps in Glandulocaudine Fishes (Teleostei: Characidae)

STANLEY H. WEITZMAN
and
SARA V. FINK

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY • NUMBER 421

SERIES PUBLICATIONS OF THE SMITHSONIAN INSTITUTION

Emphasis upon publication as a means of "diffusing knowledge" was expressed by the first Secretary of the Smithsonian. In his formal plan for the Institution, Joseph Henry outlined a program that included the following statement: "It is proposed to publish a series of reports, giving an account of the new discoveries in science, and of the changes made from year to year in all branches of knowledge." This theme of basic research has been adhered to through the years by thousands of titles issued in series publications under the Smithsonian imprint, commencing with *Smithsonian Contributions to Knowledge* in 1848 and continuing with the following active series:

Smithsonian Contributions to Anthropology
Smithsonian Contributions to Astrophysics
Smithsonian Contributions to Botany
Smithsonian Contributions to the Earth Sciences
Smithsonian Contributions to the Marine Sciences
Smithsonian Contributions to Paleobiology
Smithsonian Contributions to Zoology
Smithsonian Folklife Studies
Smithsonian Studies in Air and Space
Smithsonian Studies in History and Technology

In these series, the Institution publishes small papers and full-scale monographs that report the research and collections of its various museums and bureaux or of professional colleagues in the world of science and scholarship. The publications are distributed by mailing lists to libraries, universities, and similar institutions throughout the world.

Papers or monographs submitted for series publication are received by the Smithsonian Institution Press, subject to its own review for format and style, only through departments of the various Smithsonian museums or bureaux, where the manuscripts are given substantive review. Press requirements for manuscript and art preparation are outlined on the inside back cover.

Robert McC. Adams
Secretary
Smithsonian Institution

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY • NUMBER 421

Xenurobryconin Phylogeny and Putative Pheromone Pumps in Glandulocaudine Fishes (Teleostei: Characidae)

Stanley H. Weitzman
and Sara V. Fink

SMITHSONIAN INSTITUTION PRESS
City of Washington
1985

ABSTRACT

Weitzman, Stanley H. and Sara V. Fink. Xenurobryconin Phylogeny and Putative Pheromone Pumps in Glandulocaudine Fishes (Teleostei: Characidae). *Smithsonian Contributions to Zoology*, number 421, 121 pages, 81 figures, 4 tables, 1985.—A phylogenetic analysis of the glandulocaudine genera *Argopleura*, *Iotabrycon*, *Scopaeocharax* (new), *Tyttocharax*, and *Xenurobrycon* indicates that they form a monophyletic group, the Xenurobryconini. Their relationships to other glandulocaudine characids and the monophyly of the Glandulocaudinae remain uncertain. Hypotheses concerning the evolution and relationships of the glandulocaudine characids are reviewed and evaluated.

The phylogenetic analysis of the Xenurobryconini is based on innovative, mostly sexually dimorphic characteris in males and on reductive features of both sexes. The large number of sexually dimorphic apomorphies we list for some of the taxa is a measure of the complexity of the sexual morphology in xenurobryconins. The reductive characters are mostly reduction and/or loss of parts of the laterosensory canal system and some of the associated bones of the head and shoulder girdle. These reductions are similar to those recorded for other groups of small to minute characids but are independently derived. Usually small adult body length, reductive features, and innovative sexual characters are congruent in xenurobryconins. The described laterosensory canal reductions and certain innovative aspects of the caudal pump mechanisms may be correlated with increased resistance of water to flow encountered in these structures in small fishes of 12 to 25 millimeters in adult standard length. Our phylogenetic hypothesis indicates that reversal of laterosensory reductions to a more primitive state may occur as a correlate of reversal to a somewhat larger body size.

The phylogenetic analysis of the xenurobryconin genera indicates that *Argopleura*, whose member species attain the greatest body length of all species in the Xenurobryconini, is the most primitive morphologically and the sister group of all other xenurobryconins; that *Iotabrycon* is the sister taxon of a lineage comprising *Xenurobrycon*, *Scopaeocharax*, and *Tyttocharax*; and that *Xenurobrycon* forms a sister group to *Scopaeocharax* and *Tyttocharax*. The distributions of the genera are summarized and a three-area cladogram is presented.

Xenurobrycon was found to consist of three species: *X. marcopus* from several localities in the Rio Paraguay–Rio Paraná basin of Paraguay and Brazil; *X. pteropus*, a new species known only from Fonte Boa on the middle Rio Solimões, Brazil; and *X. heterodon*, a new species known from the Río Pachitea of eastern Peru, and from the Río Aguarico (Rio Napo drainage) and upper Río Pastaza, both of eastern Ecuador. These latter rivers are Andean tributaries of the western Amazon system. The phylogenetic relationships among the species of *Xenurobrycon* were not studied.

The anatomy of the putative pheromone pumping mechanisms in the caudal region of glandulocaudines is described and discussed. Two widely different pumping mechanisms were found, a diaphragm pump and a fin-ray pump. The first of these has at least two functionally and anatomically different forms, including a passive pump apparently operated by tail-beating during courtship display and a directly driven muscular diaphragm pump found in one subgroup of miniature xenurobryconins. The hydrodynamics of the pump systems are briefly discussed in relation to their morphology, size differences, and the resistance of water to flow in small tube-like structures.

OFFICIAL PUBLICATION DATE is handstamped in a limited number of initial copies and is recorded in the Institution's annual report, *Smithsonian Year*. SERIES COVER DESIGN: The coral *Montastrea cavernosa* (Linnaeus).

Library of Congress Cataloging in Publication Data
Weitzman, Stanley H.
Xenurobryconin phylogeny and putative pheromone pumps in glandulocaudine fishes (Teleostei : Characidae).
(Smithsonian contributions to zoology ; no. 421)
Bibliography: p.
Supt. of Docs. no. SI 1.27:421
1. Characidae—Evolution. 2. Characidae—Classification. 3. Characidae—Anatomy. 4. Pheromones. 5. Fishes—Evolution. 6. Fishes—Classification. 7. Fishes—Anatomy. I. Fink, Sara. V. II. Title. III. Title: Putative pheromone pumps. IV. Title: Glandulocaudine fishes. V. Series.
QL1.S54 no. 421 591 s [597'.52] 85-600079 [QL638.C5]

Contents

Xenurobryconin Phylogeny and Putative Pheromone Pumps in Glandulocaudine Fishes (Teleostei: Characidae)

Stanley H. Weitzman
and Sara V. Fink

Introduction

GLANDULOCAUDINE NOMENCLATURE AND HISTORY

The Glanduocaudinae is a group of American characid fish genera first recognized by Eigenmann (1914:34). Subsequently additional genera were added, subtracted, or discussed by Myers (in Eigenmann and Myers, 1929:467), Tortonese (1941–1942:77), Myers and P. de Miranda-Ribeiro (1945:6), Böhlke (1954:266, 1958a:42), Géry (1963:11), Nelson (1964a:126), Géry (1966:233), Roberts (1973:489), Fowler (1975b:332), Géry (1977:351), and Mahnert and Géry (1984:510).

Glandulocaudines are usually considered as tetragonopterine-related characids in which adult males bear modified caudal-fin scales associated with hypertrophied glandular tissue. For most species histological evidence of glandular tissue type is lacking and the grossly recognized, hypertrophied caudal tissue is simply assumed to be glandular. The presence of glandular tissue has been documented by Atkins and Fink (1979) for *Corynopoma riisei* Gill (1858:426 [66 of reprint]).

The subfamily currently consists of 17 genera and somewhat more than 40 species. The genera that have been assigned to the Glandulocaudinae are: *Corynopoma* Gill (1858:425[65 of reprint]), *Pseudocorynopoma* Perugia (1891:646), *Diapoma* Cope (1894:67), *Mimagoniates* Regan (1907:402), *Glandulocauda* Eigenmann (1911b:-168), *Hysteronotus* Eigenmann (1911b:-171), *Gephyrocharax* Eigenmann (1912:-23), *Pterobrycon* Eigenmann (1913:3), *Argopleura* Eigenmann (1913:10), *Tyttocharax* Fowler (1913:563), *Landonia* Eigenmann and Henn (in Eigenmann, Henn, and Wilson, 1914:1), *Phenacobrycon* Eigenmann (1922:147), *Acrobrycon* Eigenmann and Pearson (in Pearson, 1924:44), *Xenurobrycon* Myers and P. de Miranda-Ribeiro (1945:2), *Planaltina* Böhlke (1954:265), and *Iotabrycon* Roberts (1973:491). Below we describe a new genus, *Scopaeocharax*.

Coelurichthys A. de Miranda-Ribeiro (1908:4)

Stanley H. Weitzman, Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560. Sara V. Fink, Museum of Zoology, University of Michigan, Ann Arbor, Michigan 48109.

was synonymized with *Mimagoniates* by Eigenmann and Myers (1929:490) and by Schultz (1959:8). Nelson (1964a:63–65), however, reviewed the putative relationships and nomenclature of the species, which we here assign to *Glandulocauda* (p. 109) and *Mimagoniates*, and believed *Coelurichthys* was distinct enough to be recognized as a separate genus. We have examined numerous recently collected specimens (Appendixes 1 and 2) of all the species involved and find that *Mimagoniates microlepis* (Steindachner, 1876:7) and *Coelurichthys iporangae* A. de Miranda-Ribeiro (1908:4) may not be distinct species, and that *Mimagoniates microlepis*, *Mimagoniates inequalis* (Eigenmann, 1911b:169), *Mimagoniates lateralis* (Nichols, 1913:152), and *Mimagoniates barberi* Regan (1907:402) belong to the same genus. We therefore recognized *Mimagoniates* as the senior synonym of *Coelurichthys*. (Also see our comments under *Mimagoniates inequalis* in Appendix 2.) The species of *Glandulocauda* and *Mimagoniates* are currently under review by Menezes and Weitzman.

Stevardia Gill (1858:423 [63 of reprint]) has page precedence over *Corynopoma* Gill (1858:425 [65 of reprint]) and has been used as a valid generic name, for example by Eigenmann (1914:34) and Géry (1964:6). However, Myers (1933:11, 1934:755–756) pointed out that according to the "rule of the first revisor" of the International Commission on Zoological Nomenclature, *Corynopoma* must be the accepted name because Günther (1864:287), the first revisor, used *Corynopoma* as the senior synonym of *Stevardia* and *Nematopoma*. The latter is another generic name proposed by Gill (1858:428[68 of reprint]) for *Corynopoma*.

The monotypic *Microbrycon* Eigenmann and Wilson (in Eigenmann, Henn, and Wilson, 1914:3) has been considered or suggested as a synonym of *Pterobrycon* by Eigenmann and Myers (1929:472), Bussing (1974:136), and Géry (1977:359) but no study of this problem has been published. *Microbrycon minutus* Eigenmann and Wilson (in Eigenmann, Henn, and Wilson, 1914:3) is based on two small specimens of unknown sex. Their phylogenetic placement has not been resolved and their status remains questionable. *Microbrycon cochui* Ladiges (1950:305) was considered a junior synonym of *Tyttocharax madeirae* Fowler (1913:563) by Myers and Böhlke (1956:9), but we believe that it represents a distinct species of *Tyttocharax*, (p. 110, *Tyttocharax* sp. B). *Pristicharax* Fowler (1949:1) and *Corynopomops* Fowler (1943:6) were considered by Böhlke (1958a:45 and 50, respectively) to be synonyms respectively of *Hasemania* Ellis (1911:148) and *Gephyrocharax*. We have examined the types of these species, ANSP 72104 and ANSP 69195, and agree with Böhlke.

Fowler (1975b:333) included *Lonchogenys* Myers (1927:121) and *Nematobrycon* Eigenmann (1911a:215) in the Stevardiidae (= Glandulocaudinae), but the species of these genera do not have enlarged caudal scales or hypertrophied caudal glandular tissue. Furthermore, Fowler (1975a:67) listed *Nematobrycon* as a tetragonopterine in the first characid section of his "Catalog of World Fishes." Fowler (1975b:338) undoubtedly meant to terminate his listing of the Stevardiidae after *Tyttocharax*. However, if his list of families and subfamilies were taken at face value, his Stevardiidae includes some members of his characid subfamilies Cheirodontinae, Rhoadsiinae, Anostominae, and Prochilodinae. This inclusion may have been an oversight by the editor.

Microcaelurus A. de Miranda-Ribeiro (1939:362) was considered a synonym of *Tyttocharax* by Böhlke (1958b:319) and Mahnert and Géry (1984:512) indicated they thought its status questionable. We have examined the types of *Microcaelurus odontocheilus*, MNRJ 3572, and confirm Böhlke's referral (see Appendix 2, *Tyttocharax madeirae*).

Eight family-group names were used at one time or another for what are now called the Glandulocaudinae. These are available for several of the putative suprageneric groups of taxa within the Glandulocaudinae or as a substitute for the Glandulocaudinae. These are as follows: Stevardiinae Gill (1858:422), Diapominae Eigenmann (1910:430), Pterobryconinae Eigenmann (1913:3), Glandulocaudinae Eigenmann (1914:34), Pseudocorynopominae Eigenmann

(1914:34), Hysteronotinae Eigenmann (1914:35), Corynopominae Eigenmann (1927:395), and Xenurobryconini Myers and Böhlke (1956:6). The glandulocaudines have been recognized at the family level at times, for example the Glandulocaudidae of Fernandez-Yepez and Martin S. (1953:229) and Fernandez-Yepez and Anton (1966:67) and the Stevardiidae of Fowler (1975b:332). Myers and Böhlke (1956:6) recognized Glandulocaudini and Xenurobryconini as two of the tribes of the Characinae. Géry (1966:235, 1977:355) recognized the Glandulocaudinae as a tribe, the Glandulocaudini, separate from his Xenurobryconidi. Mahnert and Géry (1984:512–513) considered the Glandulocaudinae as probably polyphyletic and suspended judgment about the relationships of their Xenurobryconini to the Glandulocaudinae.

Priority and proper use of these names must await further study of the monophyletic lines within the Glandulocaudinae and their monophyly. The primary problem regarding the Glandulocaudinae is not its appropriate taxonomic level. Of greater concern is the question of its monophyletic or polyphyletic status and how this will affect the status of the Tetragonopterinae, a group whose monophyletic, polyphyletic, or paraphyletic nature is unresolved. In Appendix 3 hypotheses of the monophyletic nature of the Glandulocaudinae are discussed. It is concluded that there are insufficient data to resolve whether the Glandulocaudinae, as currently recognized, is monophyletic or polyphyletic. Because of these untreated problems we use these taxonomic terms, especially Glandulocaudinae, Tetragonopterinae, and Characidae, solely for convenience and do not imply acceptance of hypotheses of monophyly for these taxa.

XENUROBRYCONIN NOMENCLATURE AND HISTORY

Of the five glandulocaudine genera herein treated as members of the monophyletic group Xenurobryconini, four, *Argopleura* (Figure 1), *Iotabrycon* (Figure 2), *Xenurobrycon* (Figures 3–5), and *Tyttocharax* (Figure 6), were recognized previously. Of these four, only *Tyttocharax* and *Xenurobrycon* have been recognized as closely related. Ladiges (1950:308) recognized morphological similarities between the caudal fins of *Tyttocharax* and *Xenurobrycon* but did not investigate their relationship. Myers and Böhlke (1956:6) first suggested such a relationship and placed these two genera in a new tribe, the Xenurobryconini. Our hypothesis of xenurobryconin relationships corroborates that of Myers and Böhlke (1956) and Böhlke (1958b), as far as theirs went, but expands their Xenurobryconini to include two additional genera, *Argopleura* and *Iotabrycon.* We also recognize the species of *Tyttocharax* as treated by Böhlke (1958b) and Mahnert and Géry (1984) as belonging to two genera, the new genus *Scopaeocharax* (Figure 7) and *Tyttocharax.* Nelson (1964a:70) is the only previous author to note a similarity in the caudal scale structure of *Argopleura* and that of *Tyttocharax* and *Xenurobrycon,* but he did not investigate the possibility of a close relationship. Mahnert and Géry (1984) described briefly certain aspects of the osteology of *Xenurobrycon macropus* and *Tyttocharax madeirae* and accepted the Xenurobryconini of Myers and Böhlke (1956) but did not suggest a specific relationship between their Xenurobryconini and any other glandulocaudine.

We review the nomenclatural history of the xenurobryconin genera and examine previous hypotheses of their relationships in the section on phylogenetic hypotheses and classification. Revisionary studies of the species of *Argopleura,* *Scopaeocharax,* and *Tyttocharax* are reserved for separate publications.

Only the previously monotypic genus *Xenurobrycon* is treated at the specific level. It has been known from one collection of 17 specimens of *X. macropus* obtained in December 1941 from the Rio Bodoquena, Mato Grosso, Brazil, and from several collections from Paraguay reported recently by Mahnert and Géry (1984:498). It is a measure of how little South American freshwater fishes have been collected for systematic purposes that it was not until the last few years that further collections of these little fishes (adults

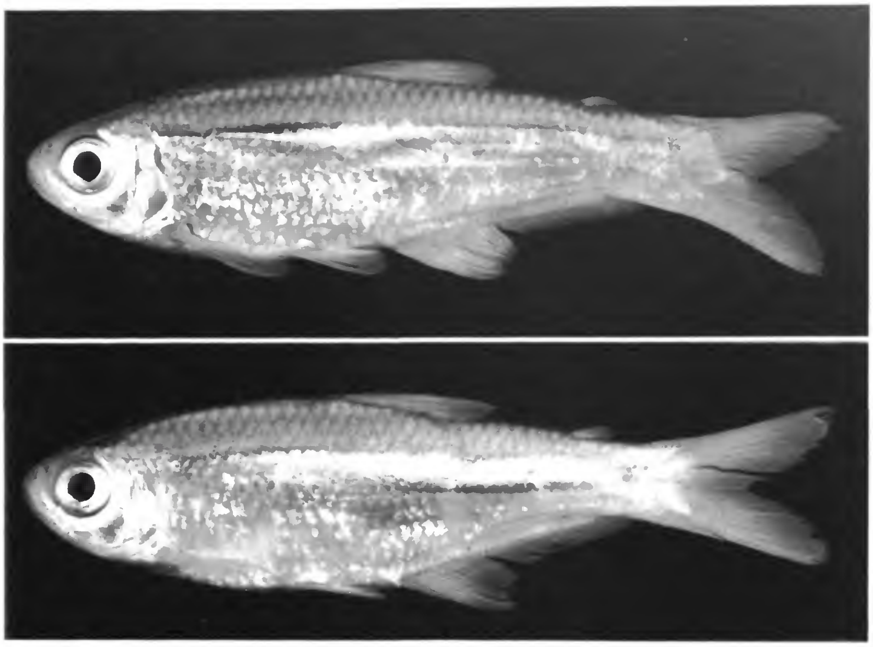


FIGURE 1.—*Argopleura chocoensis*, paratypes, CAS 39030, Colombia, Choco, Río San Juan, Istmina: *above*, male, SL 46.4 mm; *below*, female, SL 47.9 mm.

FIGURE 2.—*Iotabrycon praecox*, USNM 212065, Ecuador, Los Rios, Rio Nuevo, tributary of Río Vinces, 1 km upstream from Vinces: *above*, male, SL 17.2 mm; *below*, female, SL 17.1 mm.

Figure 3.—*Xenurobrycon macropus*, USNM 219381, Paraguay, Paraguari, Lago Ypacarai: *above*, male, SL 15.4mm; *below*, female, SL 17.1 mm.

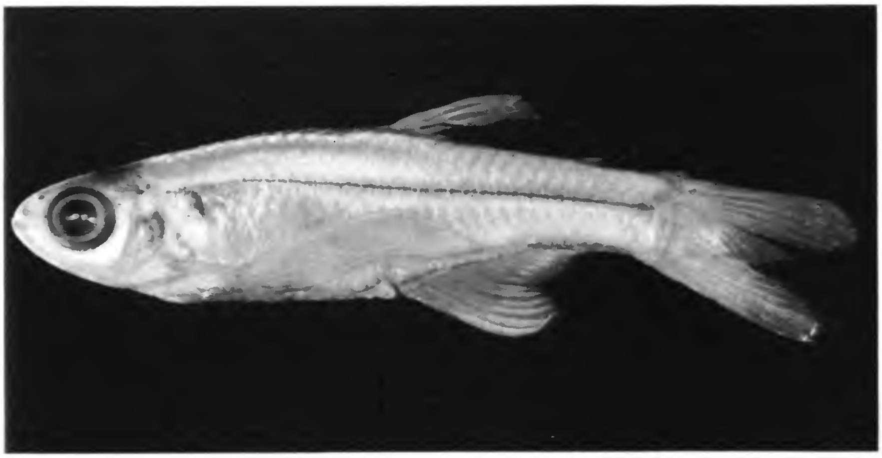


Figure 4.—*Xenurobrycon pteropus*, male, SL 13.5 mm, holotype, MZUSP 12412, Brazil, Amazonas, igarapé in Fontê Boa.

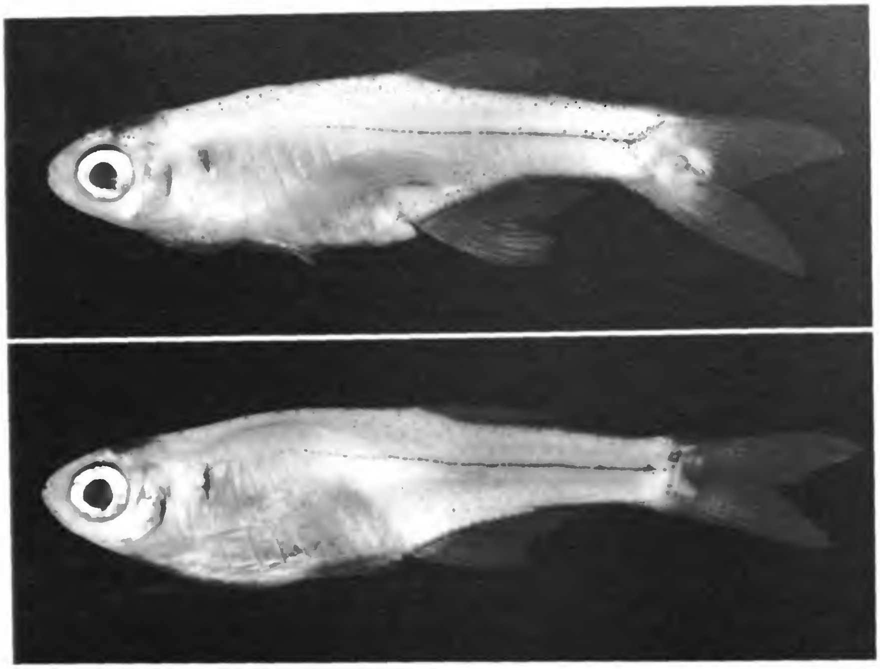


FIGURE 5.—*Xenurobrycon heterodon*, Ecuador, Pastaza, Río Bobonaza at Sarayacu: *above*, male, SL 16.2 mm, holotype, KU 17925; *below*, female, SL 16.3 mm, paratype, KU 17926.

FIGURE 6.—*Tyttocharax madeirae*, USNM 179540, Brazil, Amazonas, Rio Urubú: *above*, male, SL 15.7 mm; *below*, female, SL 14.1 mm.

FIGURE 7.—*Scopaeocharax atopodus*, USNM 217517, Peru, Huanuco, Río Huallaga at Tingo Maria: *above*, male, SL 17.9 mm; *below*, female, SL 17.8 mm.

about 12.0 to at least 17.6 mm SL) have become known. Members of the genus now appear to be widely distributed, with representatives found from the Amazon basin in Ecuador, Peru, and northern Brazil to the Rio Paraná-Rio Paraguay system of southern Brazil and Paraguay.

The original description of *X. macropus* is relatively short and now provides insufficient data for accurate species and generic distinctions or phylogenetic reconstruction. The recent redescription of *X. macropus* by Mahnert and Géry (1984:498), although more up-to-date, does not allow a detailed comparison between the three species of *Xenurobrycon* treated here. We therefore redescribe *X. macropus*, as well as describe two new species.

There has been no previous discussion of xenurobryconin biogeography, and our account is limited in scope, treating only the major generic and suprageneric groups pending further analyses of the xenurobryconin species and of the phylogenetic relationships within and among other glandulocaudine genera.

PHEROMONE CAUDAL PUMP HYPOTHESIS

Nelson (1964a:142) suggested that the caudal gland of male glandulocaudines may produce a pheromone. This hypothesis was based on his observations of courtship behavior in three glandulocaudine genera and on the morphology of the caudal glands in species of those and several additional glandulocaudine genera. Atkins and Fink (1979:469) strengthened this hypothesis for one species. *Corynopoma riisei*, noting that "In the isolated males [isolated from females], the [gland] cells were reduced in size, became densely reticulated, and stained darkly with both PAS and Alcian blue. When courtship behavior was resumed, the cells rapidly recovered their usual size and diverse staining properties." These observations indicate that the caudal gland may only function during courtship and that it may produce a pheromone.

Nelson (1964a:142) also noted that the modified fin rays of *Mimagoniates* (= his *Coelurichthys*) apparently operate as a bellows. He postulated that the caudal gland produces a substance which, when directed toward the female by this bellows during "Dusting," increases the probability that she will "Pair." Nelson further assumed the glandulocaudine tail apparatus was a passive pump associated with tail motion during courtship, facilitating dispersal of a pheromone toward the female.

Roberts (1973:494) first noted hypertrophied caudal muscle tissue in a glandulocaudine, stating that "in *Iotabrycon* the caudal modifications consist of a highly modified scale supporting a large caudal pouch and a muscle with extensive attachments to the proximal half of the upper caudal lobe." Roberts did not comment further on the function or morphology of these caudal structures.

Mahnert and Géry (1984:503) briefly considered the modified osteology and myology of the male *Xenurobrycon* and *Tyttocharax* caudal skeleton but did not hypothesize a caudal pumping mechanism.

We explore the hypothesis that most male glandulocaudines have a passive caudal pumping mechanism associated with tail-beating courtship and propose that some of the Xenurobryconini, i.e., the genera *Scopaeocharax*, *Tyttocharax*, and *Xenurobrycon*, have an active diaphragm pump, driven directly by muscles. The activity of this pump is probably also associated with tail-beating during courtship display by males. Both pumping mechanisms presumably facilitate the dissemination of a pheromone from the hypertrophied gland cells of sexually active males. Increased water flow resistance in the tiny pumps of the miniature species may be associated with the evolution of the directly driven muscular pump.

METHODS

Our methodology is phylogenetic (Hennig, 1966; Wiley, 1981). Preferred phylogenetic hypothesis are those that are most parsimonious, that is, require the fewest ad hoc assumptions about character transformations. The analysis was performed largely through Hennigian argumentation but was checked (and improved) through use of David Swofford's numerical algorithm PAUP version 2.1 (Phylogenetic Analysis Using Parsimony) on the University of Michigan Terminal System Amdahl computer.

Subjectivity in the choice of characters, traditional in phylogenetic studies, remains a prominent influence on the outcome of cladistic analyses. Our delineation of characters was done in part for descriptive ease and in part to distinguish those aspects of morphology that might have evolved separately, as independent evolutionary novelties distinguishing particular taxa. We regard our delineation, or any such delineation, as a partly unsatisfactory compromise between these two aims. The attempt to distinguish independent evolutionary novelties is a probing of the past using a highly fragmentary record. A nonarbitrary way to divide the functional and morphological attributes of an organism into subunits appropriate for phylogenetic studies has not yet been found, because of the functional and structural unity of the whole organism. These subjective aspects of character choice force weighting of characters in all phylogenetic studies.

Sober (in press) suggests that parsimony assessment in systematics can be done only with character weighting (whether equal or unequal) and, additionally, that analysis of parsimony as a likelihood technique leads to the conclusion that evolutionarily independent characters should be weighted based on whether they are labile or conservative in evolution. This conclusion accords well with some traditional systematic intuition.

We have tried to evaluate the evolutionary independence of different aspects of a "complex character" by looking at whether similar features vary independently in other taxa. While we have not weighted our characters in a in a formal way, we have tried to evaluate their conservative or labile nature in light of what is known about the distribution of similar features in related taxa. For example, we have treated as separate characters the sexually dimorphic anterior position of the pelvic girdles in males and females of subgroup B (characters 41 and 42), because the position varies independently in males and females in other xenurobryconin taxa. In both subgroup A and in *Xenurobrycon*, the position of the girdle differs from that in outgroups in males alone (characters 12 and 53). In *Scopaeocharax*, the position differs from that in outgroups in females alone (character 62). Thus the anterior position in both males and females of subgroup B may be the result of a single evolutionary event and we may be overestimating the evidence supporting the monophyly of that taxon. However, combining the male and female position as a single novelty may be a serious mistake in the other direction, leading to an underestimation.

Similarly, the separation of subgroup B male caudal morphology into various features was done in part for ease of description, both of the various parts of this complex morphology and of the homoplasies that occur relative to certain of their aspects. Perhaps equally important, subdivision into characters was done in part as an indirect method of weighting of what we perceive to be a considerable body of evidence in support of subgroup B. This perception is founded on the complexity and uniqueness of much of this morphology, and also on its apparent conservativeness (stability) in evolution. We recognize that the resulting characters are not entirely satisfactory, since they probably do not each reflect a separate evolutionary event, i.e., the independent appearance of a novelty. For example, hypertrophy of some caudal muscles and bones probably occurred together. Nevertheless, it seems unlikely that all those aspects unique to subgroup B males evolved simultaneously. While our delineation may not be historically accurate, treating this morphology as a single novelty may be even more inaccurate. Similar reasoning is applicable to some of our other "complex characters."

Polarity of character transformations (primative versus derived) is hypothesized based on outgroup comparison and on ontogenetic transformation (including sexual maturation) when the latter is available. In the absence of a higher level phylogenetic hypothesis, our outgroups cannot be narrowed to specific lineages closely related to the xenurobryconins. Therefore we have included as our outgroup a fairly complete spectrum of other glandulocaudines and a broader, but less complete, survey of American characids, especially the Tetragonopterinae. Ordinarily we assume that the later stage of a given ontogenetic transformation in a lineage is apomorphic relative to its homologue in the non-transforming group. Such a hypothesis is more parsimonious than the assumption that the secondary transformation was primitively present in the common ancestor of the groups and lost secondarily in one lineage. In cases where outgroup information indicates a secondary evolutionary loss of a transformation, we accept a loss hypothesis. In such cases the loss hypothesis correlates with other synapomorphies and the most parsimonious cladogram or hypothesis.

As explained in Weitzman and Fink (1983:350, 378–379, 388–393) there are cases in which, lacking a specific closely related outgroup, we refuse to utilize a character as a synapomorphy even if ontogenetic information indicates its possible polarity. Such situations are those where experience in related taxa shows that the character may be labile, that is, might easily have evolved in either direction during the immediate preceding evolutionary history. An increase versus a decrease in dorsal-fin and anal-fin ray numbers are examples. In characids at least, reductions and gains are often associated respectively with change toward smaller and larger adult size (see Weitzman and Fink, 1983:341–347, 391–394, for further discussions of this problem in characids). Such transformations are not easily subject to polarity hypotheses based on ontogenetic information when very closely related outgroup taxa are uncertain or unknown. This is especially true when there is variability among the outgroup taxa for similar characters, a situation that often prevails in tetragonopterine characids and nominally related groups.

In the following text we label some characters as innovative and some as reductive. We recognize as innovative characters those that have additional features beyond those present in the outgroups. Reductive characters are those associated with a loss or reduction of some particular structure present in outgroups. Reductive characters are also innovations. Nevertheless, we do not label them as such so that we may easily distinguish between these kinds of evolutionary changes.

Hecht and Edwards (1977:15) stated that the homology of loss and reductive characters is not testable by similarity since absent characters cannot be compared (see also Patterson, 1982:30–33, 44). This may be true for simple loss characters, such as absence of an adipose fin, but in characids at least, losses of cranial parts of the laterosensory system and associated bones often result in unique, new morphological patterns in the remaining proximate elements. For example, synapomorphies 4 to 7 in Weitzman and Fink (1983:354) are all innovative cranial features associated with a reduction in the laterosensory system and associated bones of the posterior region of the head of the characid genus *Paracheirodon*. Compare the posterior skull regions of characids illustrated by Weitzman and Fink (1983, figs 4–18, 29–30). When such losses are associated with new, complex, and unique similarities among related taxa, it is our opinion that a hypothesis of homology (i.e., synapomorphy) may be preposed and then analyzed for parsimonious correlation with other shared derived characters. We also use simple loss characters (such as an adipose fin loss or absence of teeth on a bone) as a synapomorphy when they correlate in a parsimony analysis with innovative synapomorphies or are part of a complex set of synapomorphies involving a particular structure or variety of structures. Many such losses have occurred in the miniature xenurobryconins. For example, synapomorphies 8 to 11 and 13 to 15 below are loss characters associated in one taxon with a few innovative structures that together form a set of synapomorphies for subgroup A.

Our approach to loss or reductive characters is essentially that explained by Weitzman and Fink (1983:343) and our approach to paedomorphosis follows that of Fink (1982).

In discussing the possible phylogenetic significance (or its absence) of characters distributed in various characid, glandulocaudine, and xenuorbryconin putative monophyletic groups, by convention the phrases "according to the most parsimonious cladogram" and "according to the most parsimonious hypothesis" have different meaning in our text. The first is reserved for discussions of homoplasy pertinent only to taxa included in our cladogram. The second is reserved for discussions of homoplasy pertinent to (or possibly affecting the monophyletic relationships of) taxa both within our cladogram and some members of the outgroups. Data corroborating the monophyly of some lineages within the outgroups are not given in great detail largely because the monophyly of few characid taxa are currently corroborated by much evidence.

The biogeogrpahic account is based on the vicariance methods and ideas suggested by Platnick and Nelson (1978) and Rosen (1978).

Glandulocaudine specimens examined are listed in Appendix 1. Most stained preparations of specimens of other characid genera and species examined for this study were listed by Weitzman (1962) and Weitzman and Fink (1983:384). For other specimens examined, museum numbers are given in the text following the name of the specimens.

Bone terminology and the use of patterned acetate overlays to identify particular bones in the drawings follows Weitzman and Fink (1983:351). The term "lateral series scales" as used in the tables and text refers to the entire lateral line series when some or all of that scale series lack laterosensory pores. In the systematic section, all measurements were made by the senior author using an ocular micrometer (reticle) measuring in tenths of a millimeter. The methods of counting and measuring are those described by Fink and Weitzman (1974:1–2). Tooth counts were taken from the left side except when noted. The word origin in reference to a fin base means the anterior basal termination of that fin. All measurements other than standard length (SL) are expressed as a percentage of SL except subunits of the head, which are expressed as a percentage of head length. Ranges, means, and 95 percent confidence limits for the means for morphometrics of the separate population samples are given in the tables. In the case of meristics, ranges, means, and standard deviations are represented by one set of figures for both males and females. The same is true for morphometrics except for cases of obvious sexual dimorphism in which the information is given by sex. Meristic information for the holotypes of all species of *Xenurobrycon* is given separately when there is variation in the count. In those cases where a value of t was computed for statistical comparison, arcsine transformations were used for morphometrics and square-foot transformations were used for counts. Arcsine transformations were used for calculating 95 percent confidence limits of the means. In analysis of covariance, logarithmic transformed data were used.

The synonymies are not meant to be complete. An attempt has been made to give complete reference to those citations which may be signficant in regard to classification or phylogeny. Generic lists such as Travassos (1952) are omitted unless they introduce a variant spelling. Only pertinent aquarium literature is cited.

ACKNOWLEDGMENTS

This study profited by James E. Böhlke's keen interest in and great knowledge of American characiform fishes, in particular the Xenurobryconini, and is dedicated to him in memory of the many enjoyable hours the senior author spent with him discussing problems concerning South America freshwater ichthyology.

The senior author is also indebted to Keith Nelson for several illuminating discussions about glandulocaudines during the late 1950s and early 1960s and for recent correspondence concerning glandulocaudine phylogeny.

We are grateful to many people who have loaned or given us specimens in their care: Federico Achaval and Raul Vaz-Ferreira, Universidad de la Republica, Uruguay; Reeve M. Bailey and Gerald R. Smith, University of Michigan Museum of Zoology (UMMZ); James E. Böhlke and Eugenia B. Böhlke, The Academy of Natural Sciences, Philadelphia (ANSP); Heraldo A. Britski and Naércio A. Menezes, Museu de Zoologia da Universidade de São Paulo (MZUSP), Brazil; William A. Bussing, Escuela de Biologia, Universidad de Costa Rica, Costa Rica; Carlos A. Gonçalves da Cruz and Oswaldo L. Peixoto, Departamento de Biologia Animal, Universidade Federal Rural do Rio de Janeiro (UFRRJ), Brazil; William Eschmeyer and Pearl Sonoda, California Academy of Sciences (CAS); William L. Fink, Museum of Comparative Zoology, Harvard (MCZ) and now of UMMZ; Jacques Géry, Argentonesse, Castels, Saint-Cyprien, France; Leda F.A. Jardim, Departamento de Zoologia, Universidade Federal do Rio Grande do Sul, Brazil; Francisco Mago-Leccia, Museo de Biología, Instituto de Zoologia Tropical, Universidad Central de Venezuela (MBUCV-V); Gustavo W. Nunan, Museu Nacional de Rio de Janeiro (MNRJ), Brazil; Donn E. Rosen and C. Laevit Smith, The American Museum of Natural History (AMNH); Pedro M. Ruiz C., Instituto de Ciencias Naturales, Museo de Historia Natural, Universidad Nacional de Colombia (ICN); Donald J. Stewart and Robert K Johnson, Field Museum of Natural History, Chicago (FMNH); and Edward O. Wiley, Natural History Museum, University of Kansas (KU). Some of the specimens collected by Donald Stewart in Ecuador were loaned to us by the Museo de Biología de la Escuela Politécnia Nacional, Quito, Ecuador, and support for their collection was provided by the Corporation Estetal Petrolera Ecuatoriana (CEPE).

Several persons and associated institutions aided this work. Paulo E. Vanzolini, Director of MZUSP, provided field support and allowed us to survey the collections in his charge. The Expedição Permanente de Amazonia (EPA), directed by Vanzolini and financed by the Fundação de Amparo a Pesquisa do Estado de São Paulo (FAPESP), supported the collection of some of the specimens used herein. Financial support for examining specimens at MZUSP and at the MNRJ, and for field collecting in Brazil and Venezuela was provided by the Smithsonian

Lowland Tropical Forest Ecosystem Research Program coordinated first by Clifford Evans and then by W. Ronald Heyer. Support for fieldwork in Brazil and Venezuela was provided by a grant from the National Geographic Society. Tuiskon Dick of the Universidade Federal do Rio Grande do Sul provided support for fieldwork in Rio Grande do Sul. Luis Pini Netto of São Paulo provided financial and logistic support for work in the Ubatuba region of São Paulo. Francisco Mago-Leccia and MBUCV provided financial and logistic support for field work in Venezuela. Gustavo W. Nunan, MNRJ, and Eugenio Izecksohn, Carlos A.G. da Cruz and Oswaldo L. Peixoto, UFRRJ, provided support for work in Rio de Janeiro (and Nunan for work in Espirito Santo). A.W. Crompton and Karel F. Liem of the Museum of Comparative Zoology, Harvard University provided space and facilities for part of the research on this project for both authors.

George V. Lauder, University of Chicago, and Karel F. Liem, Harvard University, offered advice on musculature and patiently listened to some hypotheses of the function of the caudal gland and associated structures in the glandulocaudines. Sheryl Coombs, Parmly Hearing Institute, Loyola University, Chicago, and Catherine A. McCormick, Georgetown University, Washington, D.C., listened to our hypothesis about adult size in miniature fishes and lateral-line canal reductions.

Naérico and Sílvia Menezes translated the summary into Portuguese. Barry Chernoff, Naércio A. Menezes, Keith Nelson, Wayne C. Starnes, Richard P. Vari, Anna Weitzman, and Marilyn Weitzman read the manuscript and offered valuable suggestions. Furthermore most of these individuals, as well as James E. Böhlke, William L. Fink, and Antonio Machado-Allison, have discussed characid phylogeny with one or the other or both of us numerous times and often at some length. We are grateful for their ideas and insights as they have affected our own, but of course we accept full responsibility for any errors, oversights, or differences of opinion presented herein.

George Van Dyke, Edgar N. Gramblin, Karsten E. Hartel, Robert Kanazawa, Lynn Norrod, William Saul, and especially Marilyn Weitzman have provided valuable technical assistance.

Field assistance was provided by a large number of people. Major organizational support was provided by Naércio Menezes for Brazil and Francisco Mago-Leccia for Venezuela. Actual field assistance was provided by Leonidas Aguana, Heraldo Britski, Ricardo M. C. Castro, Labbish N. Chao and his students at Fundação Universidade de Rio Grande, Rio Grande do Sul, Paulo Buckup, Leda F.A. Jardim, Carlos A. de Lucena, Z. Margarete de Lucena, Carlos A. Gonçalves de Cruz, Luiz E. de Macedo Cordoso, Rosario LaCorte, William L. Fink, Hector Lopez, Antonio Machado-Allison, Francisco Mago-Leccia, Luis Malabarba, Naérico Menezes, Luis Pini Netto, Oswaldo Peixoto, Viggo Schultz, Alexander Smart, Marilyn Weitzman, and Alicido Witeck. Garrett Glodek, Donald J. Stewart, and Richard Vari made specific and successful efforts to collect xenurobryconins for this work.

Especially Rosario LaCorte, but also Leonidas Aguana, Heraldo Britski, William A. Bussing, William L. Fink, Dan Fromm, Donald Kramer, Hector Lopez, Antonio Machado-Allison, Francisco Mago-Leccia, Naérico Menezes, David Reznick, H. Willi Schwartz, and Roberto Takase have helped capture glandulocaudines, have kept them alive in captivity, or have supplied live glandulocaudines for study. Ricardo M. Castro shared his underwater field observations of live *Glandulocauda melanogenys* and *Mimagoniates microlepis*. Ivan Sazima provided similar information for *Pseudocorynopoma heterandria*. Finally, Franz Weibezahn discussed the ecology of *Corynopoma riisei* with the senior author.

Phylogenetic Hypotheses and Classification of Xenurobryconini

In the following treatment we list and discuss various apomorphies that corroborate hypotheses of relationship among members of the Xenurobryconini. The apomorphies are numbered sequentially so that they can be identified on the cladogram (see Discussion). Within each taxonomic group the characters are ordered according to location on the body, beginning with the caudal region and ending with the jaws. Under each number a morphological description of the apomorphy is followed by separate paragraphs discussing the comparable character as found in the most appropriate outgroups available. Supplemental discussion may follow treating the morphology in more detail, any ambiguities of interpretation, and/or possible instances of convergence. Other apparent convergences that support alternate, less parsimonious hypotheses are treated in the discussion section. A few ambiguous characters are also treated in the discussion.

For named groups, synonymies with brief comments are included prior to the apomorphies.

XENUROBRYCONINI Myers and Böhlke

XENUROBRYCONINI Myers and Böhlke, 1956:6 [original description, key to and review of species].—Böhlke, 1958a:42 [considered Xenurobryconini independent of Glandulocaudinae]; 1958b:318 [expanded definition of group to include two new species of *Tyttocharax*].—Nelson, 1964a:70 [believed Xenurobryconini and Glandulocaudini related in one group, Glandulocaudinae].—Géry, 1977:362 [brief listing of recognized species, placed Xenurobryconini following Glandulocaudini in his Glandulocaudinae].—Mahnert and Géry, 1984:512 [definition of group and discussion of relationships].

XENUROBRYCONIDI Géry, 1963:11 [alternate spelling (suffix) for Xenurobryconini]; 1965b:195 [listed].

The Xenurobryconini as first described by Myers and Böhlke (1956:6) comprised only *Tyttocharax* and *Xenurobrycon*. Böhlke (1958b) described two new but rather different species of *Tyttocharax* (here placed in *Scopaeocharax*) and included them in the Xenurobryconini (equivalent to our subgroup B). Our expansion of the Xenurobryconini to include *Argopleura* and *Iotabrycon* is based on a series of five synapomorphies, all sexually dimorphic, and all but one, a pelvic-fin character, found in the caudal region of the males. All caudal synapomorphies are associated with the putative pheromone-producing apparatus of the males.

Böhlke (1958a, and in discussion with the senior author) did not consider the xenurobryconins (sensu Myers and Böhlke) and the glandulocaudines to be closest relatives, primarily because of tooth structure. He believed the simple conical teeth of the Xenurobryconini, as understood in 1958, to be an important consideration for the recognition of monophyly of characid subgroups. Once he learned from us that an undescribed species of *Xenurobrycon* had some tricuspid teeth, his objections to a xenurobryconin-glandulocaudine relationship vanished, although he beleived as we do that the monophyly of Glandulocaudinae remains unresolved. Mahnert and Géry (1984:512) were confident of the monophyly of the Xenurobryconini (sensu Myers and Böhlke) but were uncertain about its relationships to any other glandulocaudines.

The following five synapomorphies are diagnostic for the Xenurobryconini and corroborate the hypothesis that the glandulocaudine genera *Argopleura*, *Iotabrycon*, *Xenurobrycon*, *Tyttocharax*, and *Scopaeocharax* are more closely related to one another than to any other glandulocaudines or characids.

1. The parhypural and hypural 1 are fused to each other in sexually mature male xenurobryconins (Figures 8–14).

In other glandulocaudines (Figures 15–20) this fusion is absent. It is also absent in females of all xenurobryconins except *Iotabrycon praecox* (synapomorphy 19). Most other characids, such as *Brycon meeki* (Figure 21), have these elements unfused.

Some serrasalmine characids have the parhypural and hypurals 1 and 2 fused together in both sexes. Such fusion is not characteristic of most serrasalmines. *Brittanichthys axelrodi* Géry, a small (often less than 20 mm SL as an adult) apparently tetragonopterine characid from the Rio Negro, Amazonas, Brazil, has the parhypural and hypurals 1, 2, and 3 fused to a single element in males. Since the relationships of *Brittanichthys* are unknown, such fusion suggests a need for exploring a relationship with the xenurobryconins. Males of *Brittanichthys* also have modified caudal-fin rays, but the form and shape of these are unique to the genus and very different in

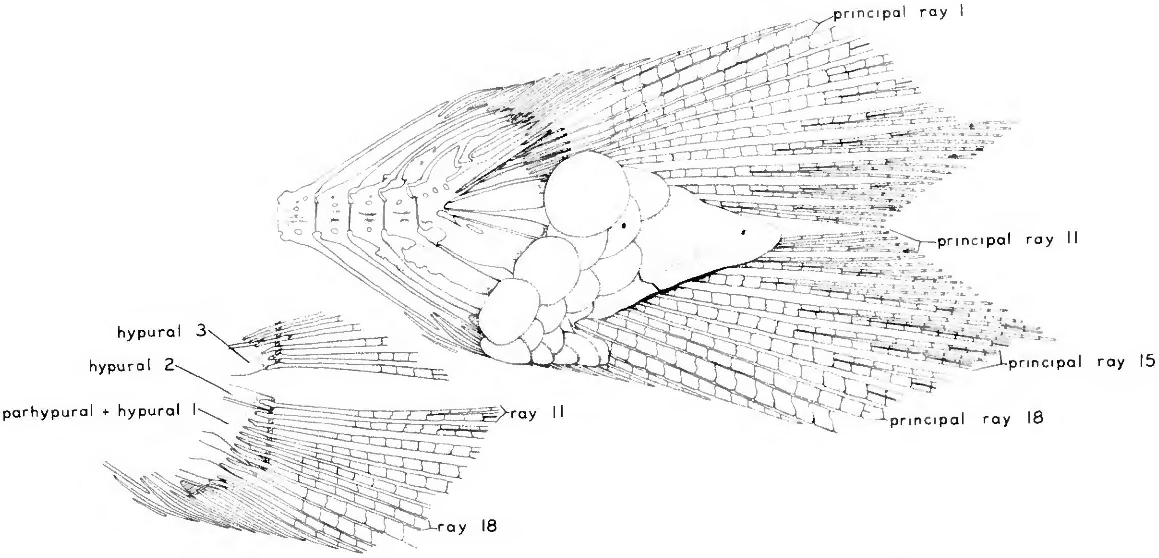


FIGURE 8.—*Argopleura chocoensis*, caudal skeleton (lateral view, left side), male, SL 45.5 mm, paratype, CAS 39030, Colombia, Choco, Río San Juan, Istmina. Two pouch scales and associated caudal squamation shown in large figure at right; these scales removed in inset at lower left.

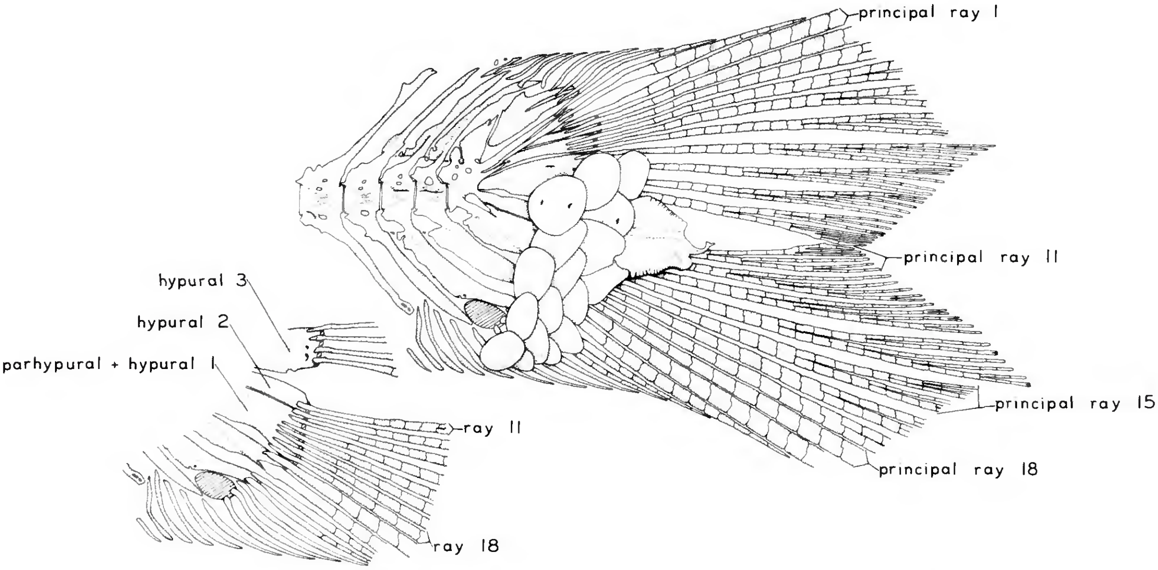


FIGURE 9.—*Argopleura* sp. caudal skeleton (lateral view, left side), male, SL 42.3 mm, ANSP 127516, Colombia, Caldas, Río Mercedes. Two large pouch scales and associated caudal squamation shown in large figure; these scales removed in inset at lower left. Posterior terminal process of pouch scale serves as attachment for ligament to principal ray 11.

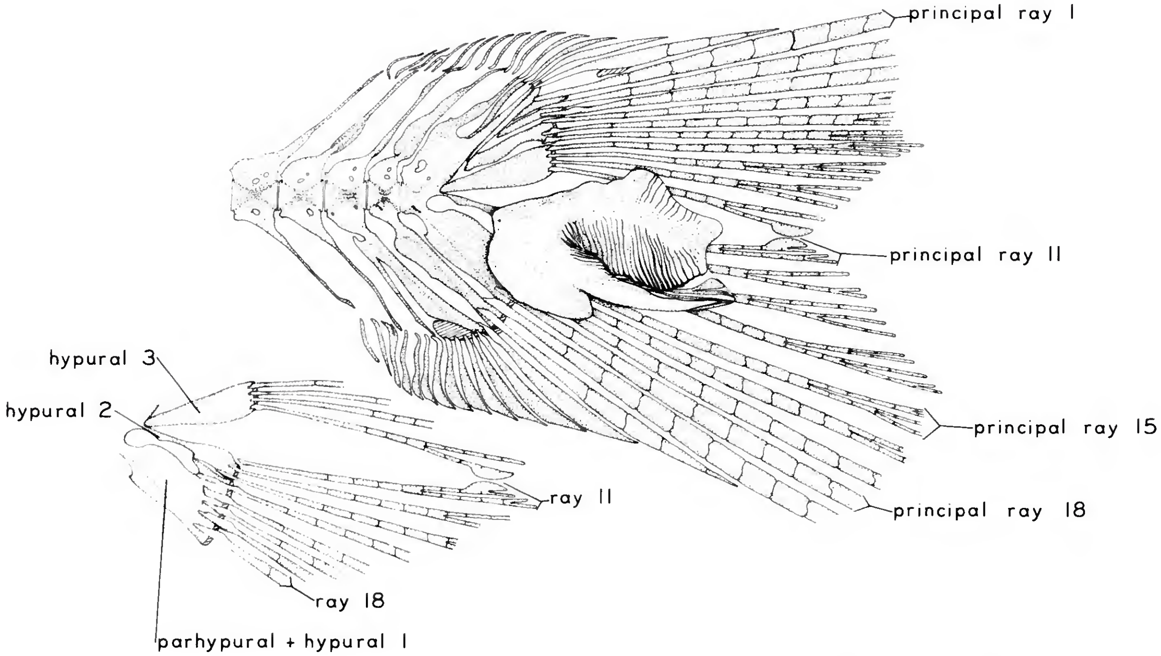


FIGURE 10.—*Iotabrycon praecox*, caudal skeleton (lateral view, left side), male, SL 21.5 mm, USNM 216802, Ecuador, Los Rios, Río Palenque. Pouch scale removed in inset at lower left.

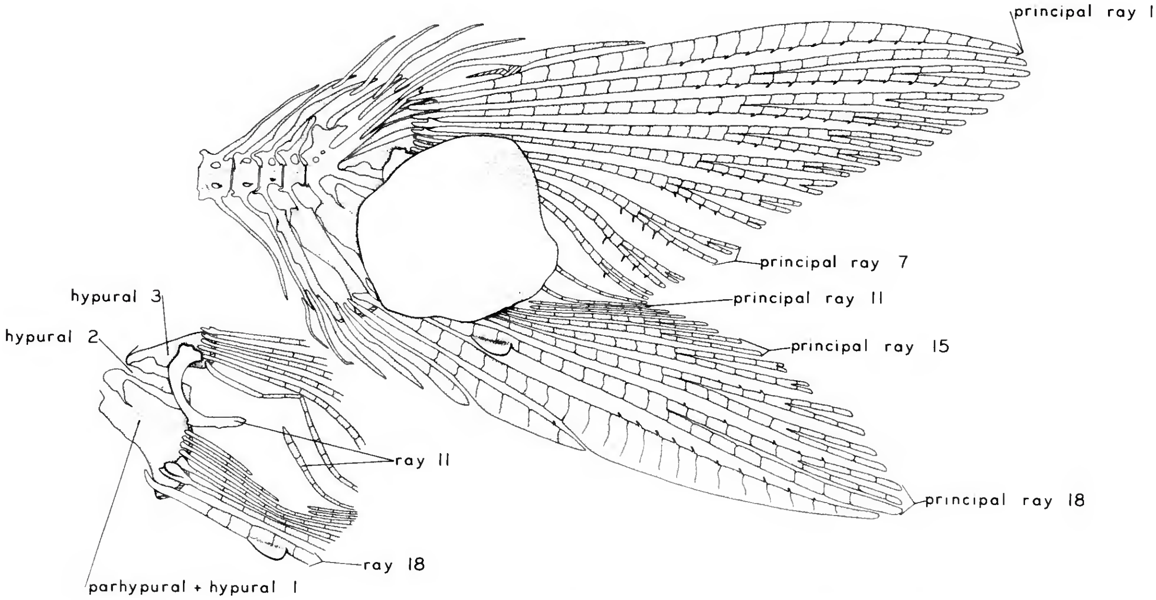


FIGURE 11.—*Xenurobrycon macropus*, caudal skeleton (lateral view, left side), male, SL 14.4 mm, USNM 219381, Paraguay, Paraguari, Lago Ypacarai. Pouch scale present in large figure; pouch scale removed in inset at lower left. Actual overlap of dorsal lobe onto ventral lobe not shown so that all fin rays may be seen. Inset at lower left illustrates structures deep to pouch scale.

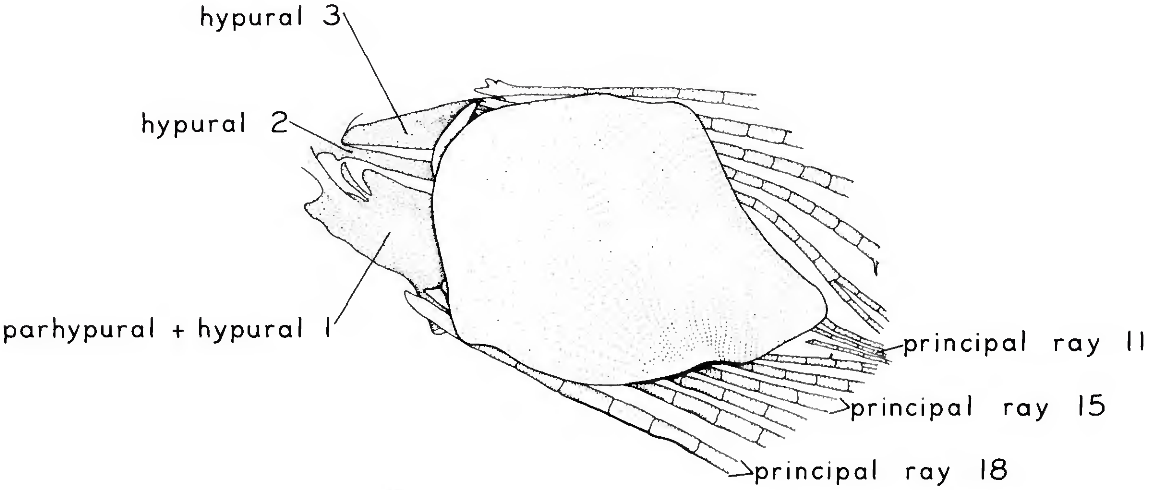


FIGURE 12.—*Xenurobrycon heterodon*, pouch scale and surrounding skeletal structures (lateral view, left side), adult male, SL 16.4 mm, USNM 219390, Ecuador, Pastaza, Río Bobonaza.

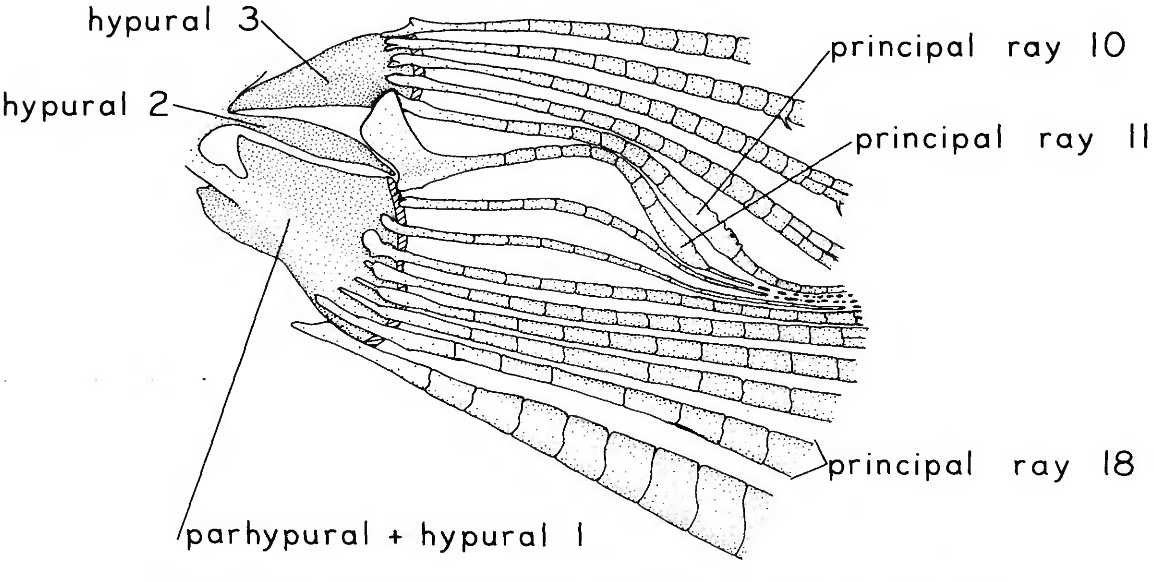


FIGURE 13.—*Scopaeocharax atopodus*, part of caudal skeleton with pouch scale removed (lateral view, left side), male, SL 21.1 mm, USNM 207517, Peru, Huanuco, Río Huallaga, Tingo Maria. Thickened portions of 10th ray and 11th ray (=sigmoid ray) serve as attachment for ligament from pouch scale; actual overlap of dorsal caudal-fin lobe onto ventral lobe not illustrated so that all fin rays may be seen.

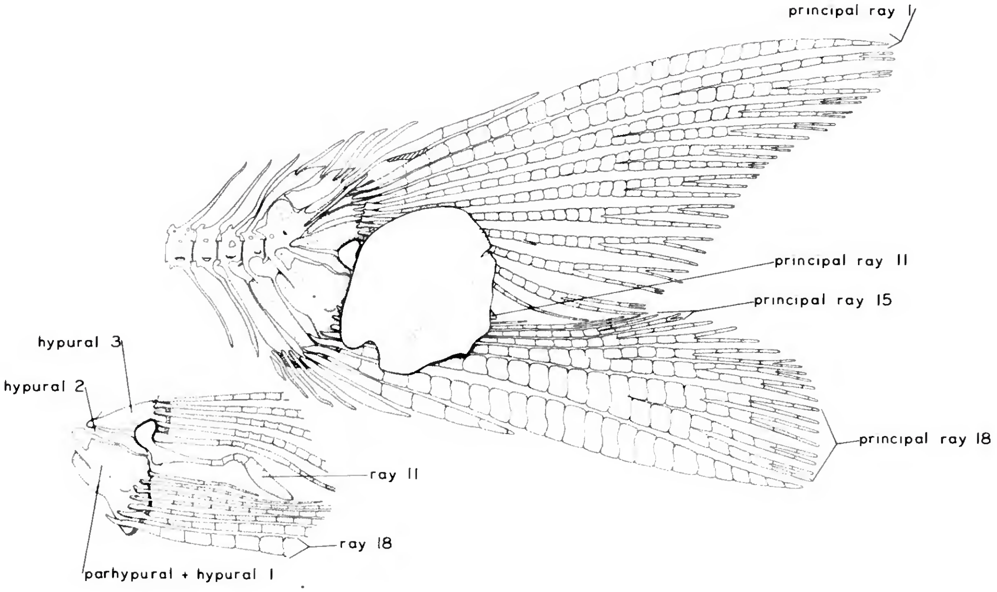


FIGURE 14.—*Tyttocharax madeirae*, caudal skeleton (lateral view, left side), male, SL 15.4 mm, USNM 179540, Brazil, Amazonas, Rio Urubú. Actual overlap of dorsal lobe rays onto ventral lobe not shown so that all fin rays may be seen. Inset at lower left with pouch scale removed to reveal sigmoid ray (principal ray 11). Thickened portions of principal rays 10 and 11 form attachment for ligament from large caudal scale.

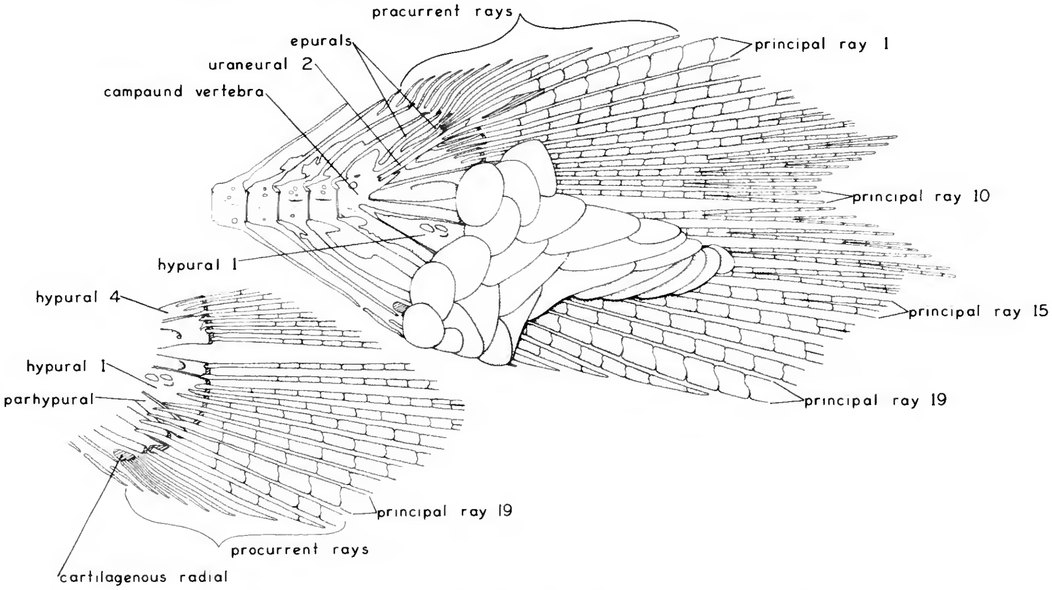


FIGURE 15.—*Diapoma speculiferum*, caudal skeleton (lateral view, left side), male, SL 30.2 mm, USNM 236094, Brazil, Rio Grande do Sul, Rio Forqueta at Marquês de Souza. Pouch scales and associated caudal squamation shown in large figure at right; these are removed in inset at lower left.

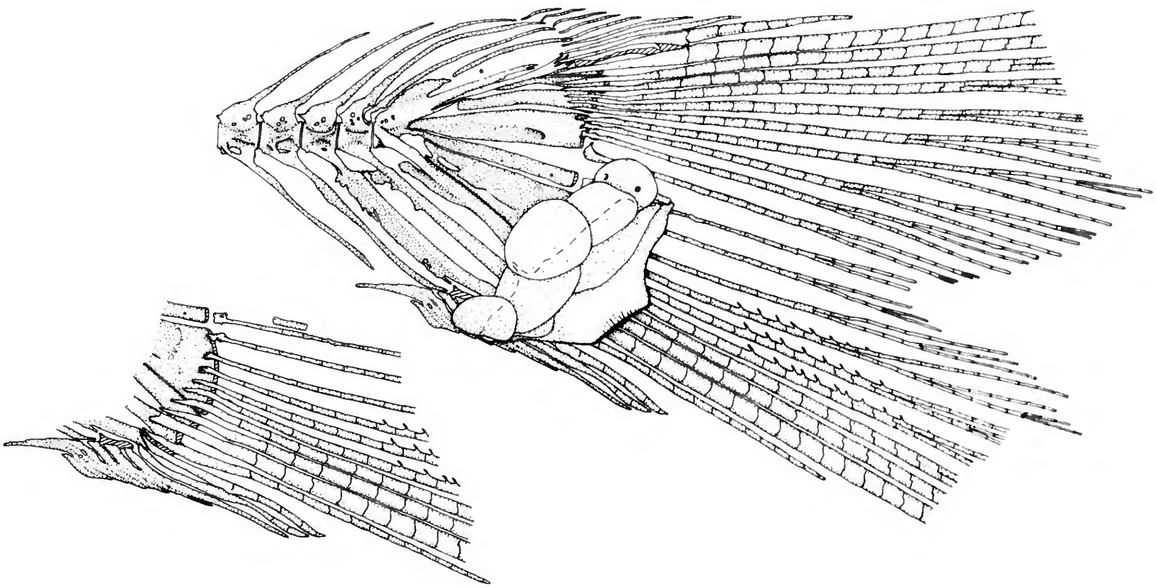


Figure 16.—*Corynopoma riisei*, caudal skeleton (lateral view, left side), adult male, SL 36.4 mm, USNM 221171, Venezuela, Carabobo, Río Chirgua. Large pouch scale and associated caudal squamation shown in large figure at right; these are removed in inset at lower left. Terminal lateral-line tube shown in its entirety in inset.

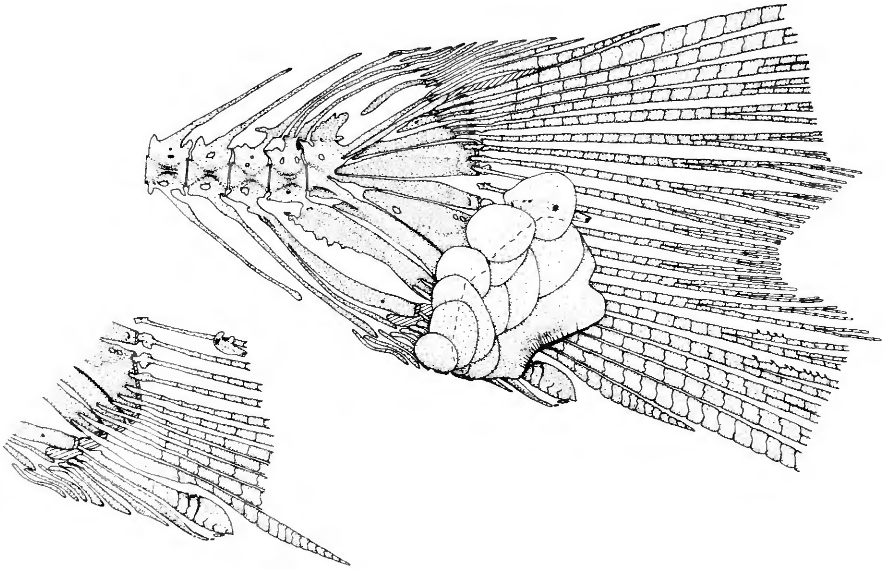


Figure 17.—*Gephyrocharax atricaudatus*, caudal skeleton (lateral view, left side), adult male, SL 47.4 mm, USNM 236086, Panama, 13 km north of Cerro-Azul. Large pouch scale and associated caudal squamation shown in large figure at right; these are removed in small inset, lower left. Terminal lateral-line scale shown in its entirety in inset.

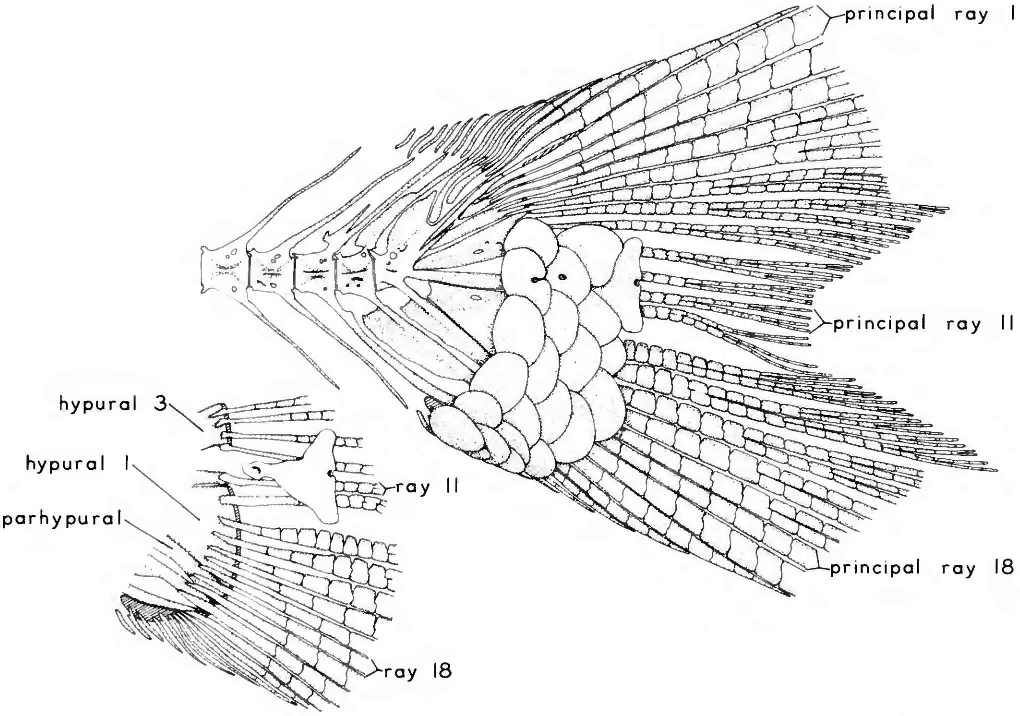


FIGURE 18.—*Landonia latidens*, caudal skeleton (lateral view, left side), adult male, SL 36.1 mm, MCZ 48663, Ecuador, Los Rios, Río Vinces at Vinces. Modified terminal lateral-line scale shown in its entirety in inset. Space between rays 12 and 13 marks position of modified bilateral caudal tissue.

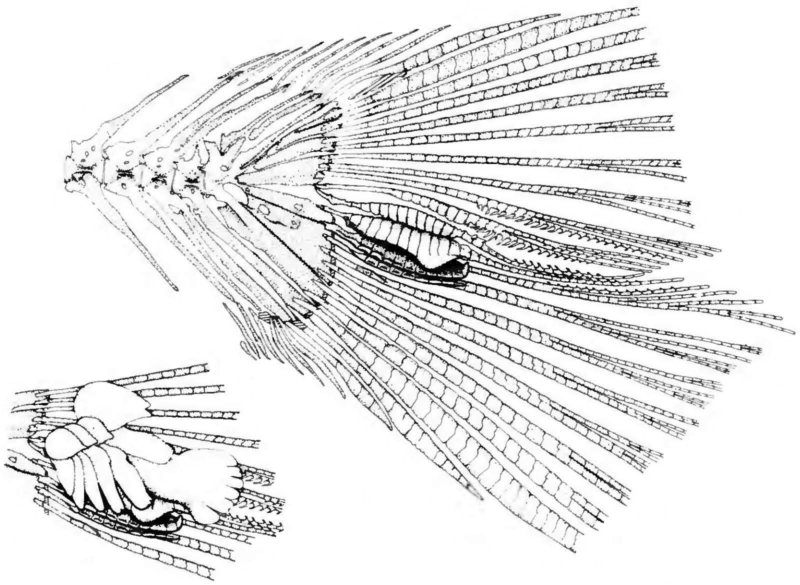


FIGURE 19.—*Mimagoniates microlepis*, caudal skeleton (lateral view, left side), male, SL 45.3 mm, USNM 236089, Brazil, Paraná, Rio Nhundiaquara at Morretes. Modified squamation illustrated in inset.

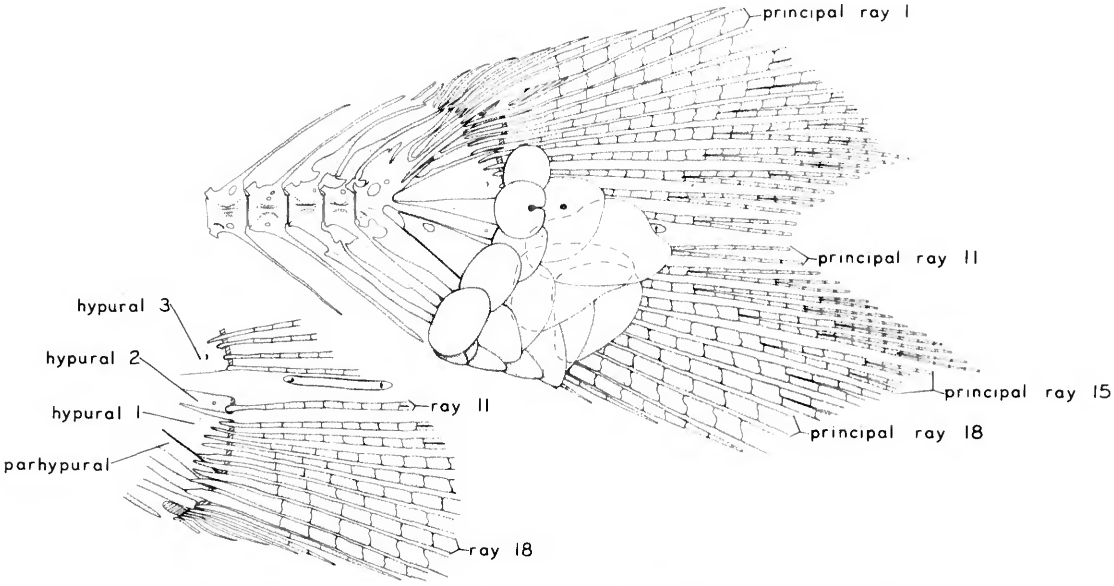


FIGURE 20.—*Phenacobrycon henni,* caudal skeleton (lateral view, left side), adult male, SL 30.2 mm, MCZ 48660, Ecuador, Los Rios, near Vinces. Obscured borders of three hypertrophied ventral lobe scales shown in dashed lines; terminal lateral-line tube shown in inset.

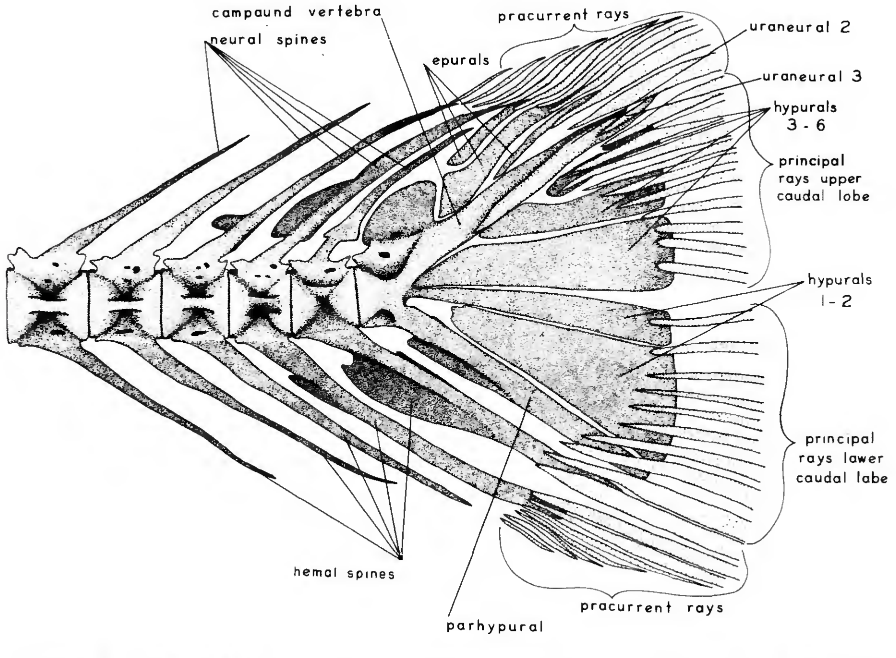


FIGURE 21.—*Brycon meeki,* caudal skeleton (lateral view, left side), juvenile, SL 82.0 mm, CAS(IUM) 12984, Colombia, Nariño, Rio Telembi, tributary of Río Patia near Barbacoas. Structure labeled compound vertebra consists of first preural centrum, its arch, ural centra, and first uroneural of ural centra; compound vertebra fused with parhypural.

form from those of any xenurobryconin or other glandulocaudine. Compare the caudal skeleton of glandulocaudine characids (Figures 8–20) with that of *Brittanichthys* in Géry (1965a, figs. 2, 6). The suggestion of relationship with the xenurobryconins is contradicted by the fact that *Brittanichthys* males lack a caudal gland and the modified caudal squamation found in male glandulocaudines. Thus, the most parsimonious hypothesis of the character distributions among these fishes indicates that fusion between the parhypural and hypural 1 has evolved independently within serrasalmines, in the Xenurobryconini, and probably in *Brittanichthys* as well.

Roberts (1973, fig. 25) illustrated a specimen of *Iotabrycon praecox*, 18.8 mm SL, MCZ 48659. This specimen has the parhypural and hypural 1 fused. Most of the line in Roberts' figure that appears to separate these bones demarcates thicker, more deeply stained bone from thinner, lightly stained bone. None of the line is a joint line separating the parhypural and hypural 1. This same specimen has hypurals 1 and 2 fused anteriorly for about two-thirds of their length. Based on Roberts' figures, Mahnert and Géry (1984:510) concluded that such morphology was representative of male *Iotabrycon*. Of the nine alizarin preparations of *Iotabrycon praecox* examined for the present study, the specimen illustrated by Roberts was the only one with any fusion between hypurals 1 and 2. Such fusion is therefore not characteristic of *Iotabrycon*.

2. In sexually mature males the distance between the articular bases of principal caudal-fin rays 10 and 11 is greater than the vertical length of the posterior margin of hypural 3 (Figures 8–11). This character is reversed in subgroup C (apomorphy 56; Figures 13, 14).

In other glandulocaudines, other characids, and in female xenurobryconins the distance in males (and females) between the bases of rays 10 and 11 is distinctly less than the length of the posterior margin of hypural 3 (Figures 15–21).

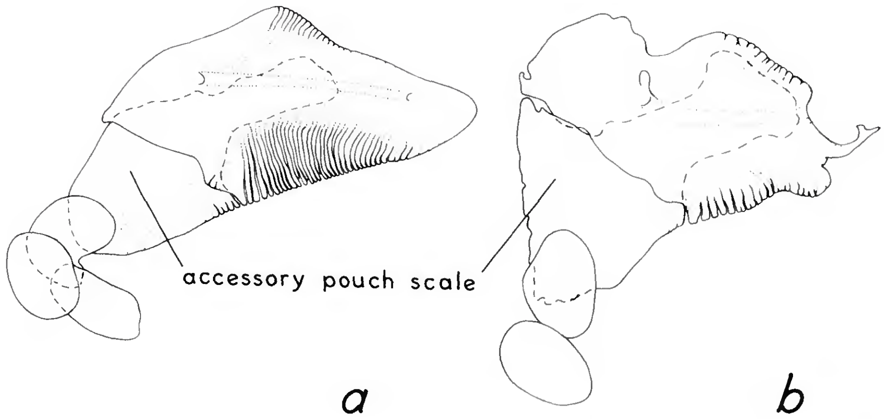
3. The terminal lateral-line scale of sexually mature males (subsequently called the pouch scale) is much larger than the same scale of the mature female and immatures of both sexes. The scale is hypertrophied on all its borders. The greatest hypertrophy occurs in the posterior field, which is large and bears numerous radial striae. The posteroventral border of this field bears between 25 to 100 striae and its posterodorsal border bears from 12 to 65. Note that the ventral border of this scale in *Iotabrycon praecox* bears an elongate posterior process, which projects ventral to the ventral fimbriated border of the hypertrophied posterior field (Figures 23, 32; apomorphy 21). The dorsal border always has fewer striae than the ventral border in any given individual specimen of any species (Figures 22–33). Along the posteroventral border of this field and dorsally into part of the scale body, the radial striae are modified so that they completely separate the ventral part of the field into strips of bone joined to each other by soft connective tissue.

Of the xenurobryconin genera only *Argopleura* has a laterosensory canal in the pouch scale, a primitive character for the Xenurobryconini. Evidence that the large caudal scale of *Iotabrycon*, *Scopaeocharax*, *Tyttocharax*, and *Xenurobrycon* is the homologue of the terminal lateral-line scale of *Argopleura* is as follows. The scale is located at the posterior end of the same horizontal scale row that bears the complete lateral line in *Argopleura*. This row bears only a few anterior pored scales in the other four xenurobryconin genera. The large scale in these genera, as in *Argopleura*, always bears a close physical association (often elaborated) with the interradialis muscles and principal caudal-fin rays 10 and 11. In no other glandulocaudine does the large pouch scale or scales have this association. These structural relationships are discussed further under apomorphy 4.

A pouch is present medial to this hypertrophied scale in sexually mature males. The opening of the pouch occurs along the ventral border of the posterior field of the scale. The majority of the bony fimbriae formed by the radii of the scale occur in this part of the lateral pouch wall. The fimbriae may provide vertical strength and stiffness and horizontal flexibility to the wall.

The pattern of development of the pouch scale can be ascertained by comparing the adult pouch scales of *Argopleura chocoensis* (Figure 22*a*) and of *Xenurobrycon heterodon* (Figure 30), with the developing pouch scales of *Xenurobrycon macropus* (Figure 31) and *Iotabrycon praecox* (Figure 32). The pouch scale of species of *Argopleura* has a lateral-line tube extending longitudinally across almost the entire scale and dividing the scale into dorsal and ventral fields. A lateral-line tube is absent in *Xenurobrycon heterodon* and *X. macropus*, but the dorsal and ventral fields are quite distinct. Comparing the distribution of circuli and radii on the pouch scale of adult *Xenurobrycon heterodon* (Figure 30) and the developing pouch scale of *Xeneurobrycon macropus* (Figure 31) indicates how the hypertrophied posterior field develops. As the scale grows posteriorly, radii apparently increase by appearing between radii already present and by being added near the posterior end of the growing scale (see also apomorphy 32).

A second modified scale, the terminal scale of the scale series two horizontal rows ventral to the lateral-line series



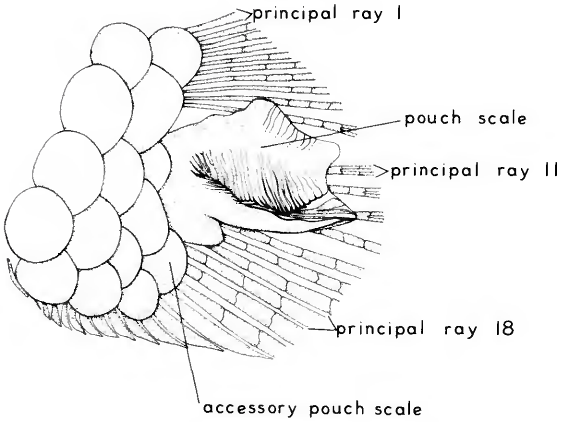
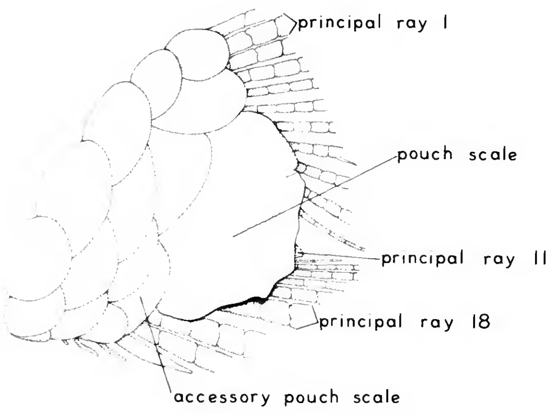


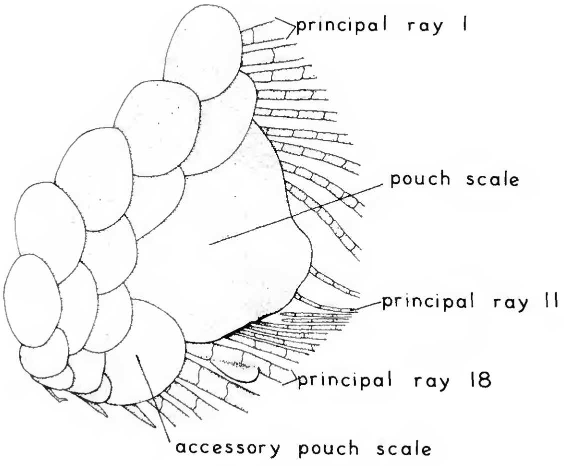
FIGURE 22 (top).—Pouch scales and ventrally associated scales (lateral view, left side): *a*, *Argopleura chocoensis*, adult male, SL 45.5 mm, paratype, CAS 39030, Colombia, Choco, Rio San Juan; *b*, *Argopleura* sp., male, SL 42.3 mm, ANSP 127516, Colombia, Caldas, Río Mercedes. Hidden scale borders shown by dashed lines.

FIGURE 23 (center).—*Iotabrycon praecox*, pouch scale, surrounding fin rays and squamation (lateral view, left side), adult male, composite mainly based on specimen SL 17.7 mm, MCZ 50602, but some details added from MCZ 216802, both specimens from Ecuador, Los Rios, Río Palenque.

FIGURE 24 (bottom left).—*Tyttocharax madeirae*, pouch scale, surrounding fin rays, and squamation (lateral view, left side), male, SL 15.4 mm, USNM 179540, Brazil, Amazonas, Rio Urubú.

FIGURE 25 (bottom right).—*Xenurobrycon macropus*, pouch scale, surrounding fin rays, and squamation (lateral view, left side), male, SL 14.4, mm, USNM 219381, Paraguay, Paraguari, Lago Ypacarai.





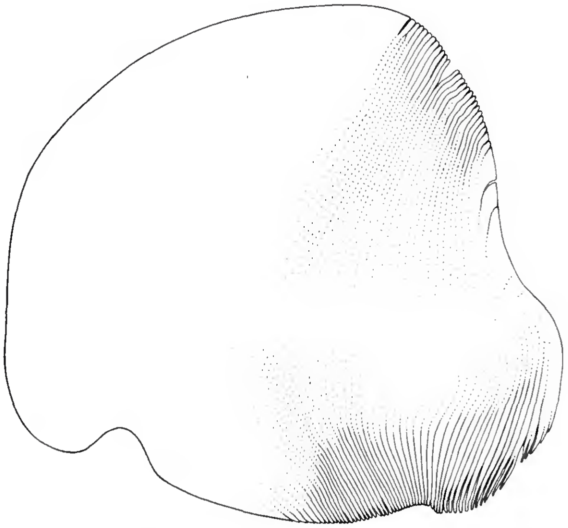


FIGURE 26.—*Scopaeocharax atopodus*, pouch scale, illustrating distribution of radii (lateral view, left side), adult male, SL 21.1 mm, USNM 207517, Peru, Huanuco, Río Huallaga, Tingo Maria.

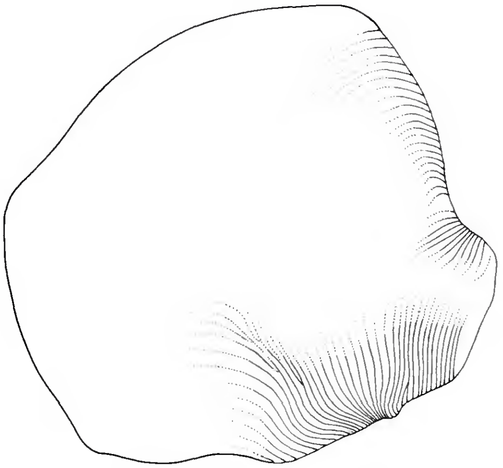


FIGURE 28.—*Xenurobrycon macropus*, pouch scale, illustrating distribution of radii (lateral view, left side), adult male, SL 14.4 mm, USNM 219381, Paraguay, Paraguari, Lago Ypacarai.

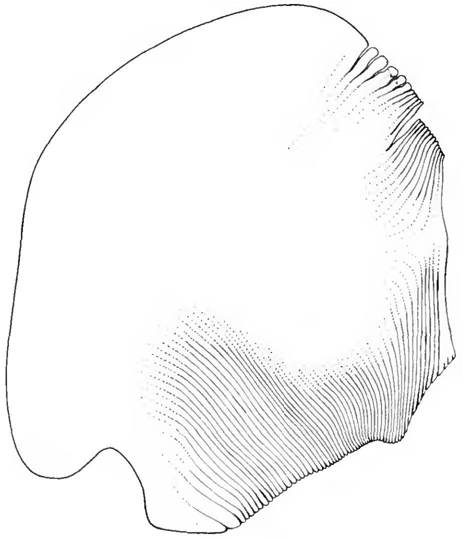


FIGURE 27.—*Tyttocharax madeirae*, pouch scale, illustrating distribution of radii (lateral view, left side), adult male, SL 15.4 mm, USNM 179540, Brazil, Amazonas, Rio Urubú.

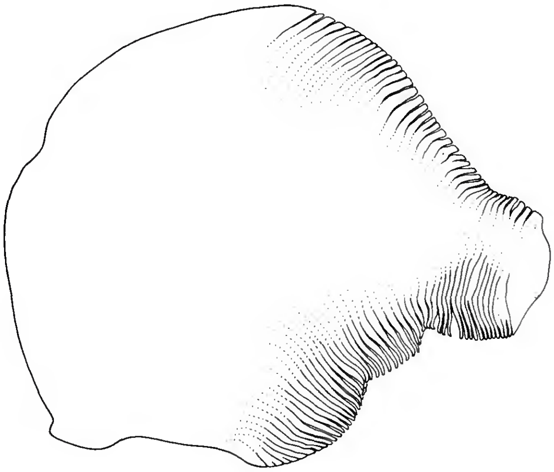


FIGURE 29.—*Xenurobrycon pteroptus*, pouch scale, illustrating distribution of radii (lateral view, left side), adult male, SL 13.8 mm, paratype, USNM 232921, Brazil, Amazonas, igarapé in Fonte Boa.

(with or without pores), occurs in close association with the pouch scale and, except in *Iotabrycon* (apomorphy 21), near the anterior region of the pouch opening. This accessory pouch scale bears radial striae similar to the striae of the pouch scale, for example in *Argopleura chocoensis* (Figure 22*a*), *Tyttocharax madeirae* (Figure 24), and *Xenurobrycon macropus* (Figure 25). The accessory pouch scale in *Iotabrycon* bears 7 or 8 radii on its posterior field. These radii are larger and more clearly defined than on any other scale except the pouch scale.

Other glandulocaudines and characids with pored lateral-line scales in the caudal region have the terminal lateral-line scale either similar to the other lateral-line scales, or consisting primarily of a bony tube, occasionally with a small amount of platelike bone attached to the tube (Figures 16–18). Most other glandulocaudine males (and females in a few species) have one or more large caudal scales and some of these fishes, such as *Corynopoma riisei* (Figure 16) and *Gephyrocharax atricaudata* (Figure 17), have hypertrophied radii along the ventral border of one or more of these large scales. These radii are also associated with the pouch's lateral wall and the opening of the pouch occurs at the scale's ventral border. However, these pouch scales are never the terminal scales of the lateral-line seris and, in all but *Pseudocorynopoma*, are without a posterior hypertrophied field or process.

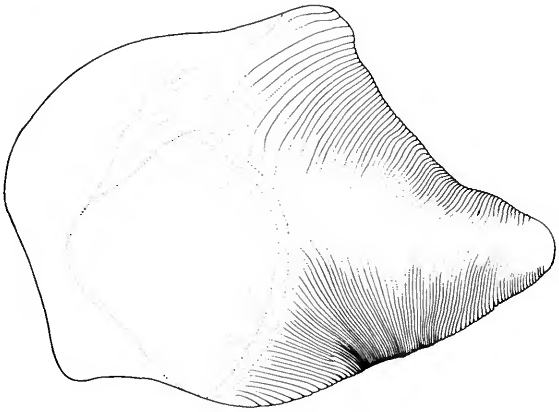


FIGURE 30 (top).—*Xenurobrycon heterodon*, pouch scale (lateral view, left side), adult male, SL 16.4 mm, USNM 219390, Ecuador, Pastaza, Río Bobanaza. The radial and circular inscriptions of the main body of the scale are shown. The greatly developed posterior lobe of this species has nearly 90 radii along its ventral border. (See text for explanation of growth pattern.)

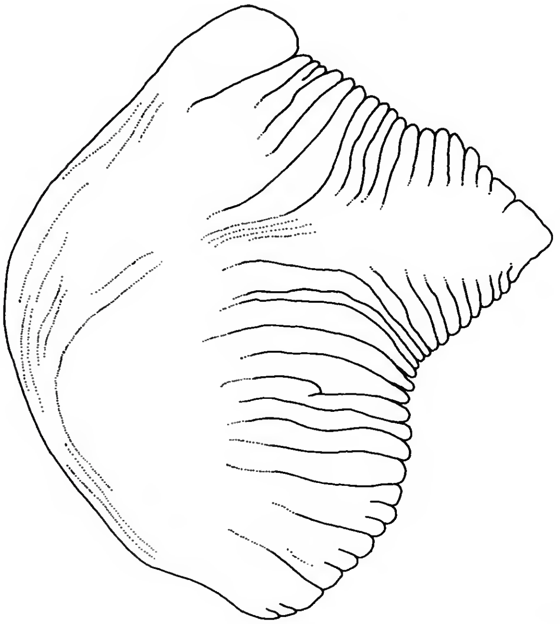


FIGURE 31 (center).—*Xenurobrycon macropus*, developing pouch scale (lateral view, left side), male, SL 14.7 mm, UMMZ 205412, Paraguay, La Cordillera, Arroyo Tobati. Developing radii shown complete; circuli incompletely represented in anterior region of scale by dotted lines.

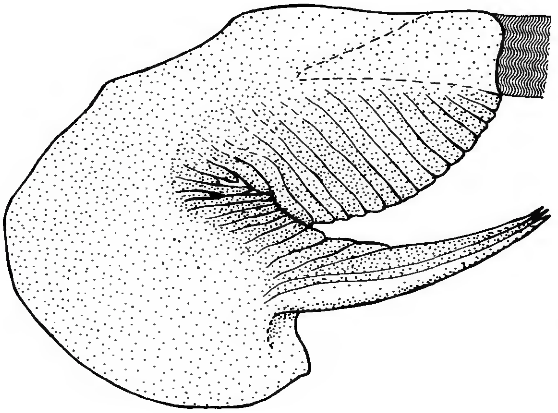


FIGURE 32 (bottom).—*Iotabrycon praecox*, developing pouch scale (lateral view, left side), male, SL 14.7 mm, USNM 236064, Ecuador, Los Rios, Río Palenque. No circuli present, developing radii shown complete. Anterior portion of ligament attaching scale to ray 11 shown at upper right. Ventral border of ligament and anterior border of ligament medial to scale shown by dashed line.

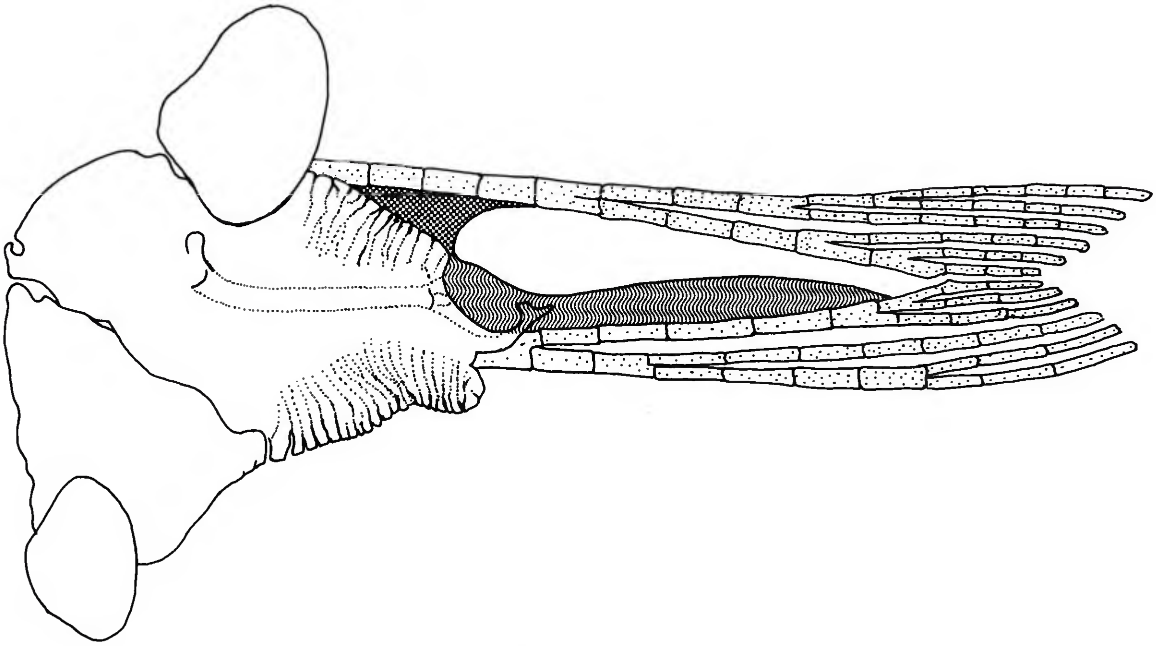


FIGURE 33.—*Argopleura* sp., pouch scale, associated scales, and fin rays 10 and 11 (lateral view, left side), adult male, SL 42.3 mm, ANSP 127516, Colombia, Caldas, Rio Mercedes. Ligament attaching posterior end of pouch scale to ray 11 shown by pattern of wavy lines. Relatively thin connective tissue, shown by heavy stipple, also attaches dorsoposterior part of pouch scale to ray 10. This tissue of each side encloses a median dense pad of connective tissue attached to ventral border of ray 10, and dorsal border of pouch scale. Dense connective tissue apparently acts as a cushion preventing direct bony contact between scales and ray 10.

Based on tentative phylogenetic hypotheses regarding these other glandulocaudines and the fact that different scales are modified in non-xenurobryconin glandulocaudines, we suggest that the presence of a greatly hypertrophied scale, radii, and posterior scale field in these other taxa are convergent with the similar features in xenurobryconins.

A terminal lateral-line scale with two platelike wing-shaped processes is present in males of the monotypic *Landonia latidens* Eigenmann and Henn, a putative glandulocaudine (Figure 18). However, this scale lacks the hypertrophied posterior field, hypertrophied radii, and border forming an opening of a caudal pouch, featurs found in xenurobryconins.

The monotypic *Phenacobrycon henni* Eigenmann, another putative glandulocaudine, could be interpreted as having an enlarged terminal lateral-line scale in males. The caudal region of *Phenacobrycon henni* (Figure 20) bears several large ventral caudal-lobe scales. The dorsalmost hypertrophied scale might be considered a lateral-line scale that has lost its lateral-line pore since it is associated with principal caudal-fin rays 10 and 11. However, the anterior border of this scale inserts into the scale row just ventral to the lateral-line series. The bony terminal lateral-line tube, although largely medial to this scale, is a completely separate element, and the shape of this scale indicates that its dorsal border has invaded or grown into the area superficial to the lateral-line tube. Furthermore, the posterior borders of the enlarged scales in the one undamaged unstained male available to us, MCZ 48661, SL 27.1 mm, are posteriorly not free of the fin rays and we find no pouch or pocket associated with these scales. We interpret this large scale as not homologous with the terminal lateral-line scale of the Xenurobryconini and as belonging to the scale row ventral to that of the lateral line.

4. In sexually mature males a strong ligament binds the posterior part of the pouch scale to principal caudal-fin ray 11 or to rays 10 and 11 (Figures 32–34). The ligament is cordlike in the more primitive genera but is broad, thick, and quite short in some of the more specialized genera. In *Xenurobrycon* it is relatively weak compared to other xenurobryconins and divided horizontally into two parts (see also apomorphies 50, 55, 58, 59).

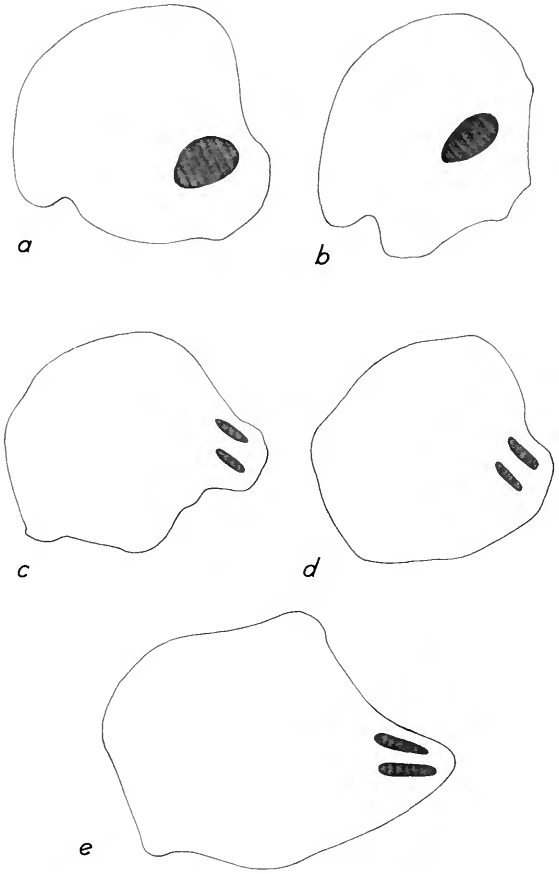


FIGURE 34.—Subgroup B, xenurobryconins, profile of pouch scales (lateral view, left side), illustrating areas of medial attachment of pouch scale ligaments (inner ellipsoids enclosing wavelike pattern): *a, Scopaeocharax atopodus*, USNM 207517; *b, Tyttocharax madeirae*, USNM 179540; *c, Xenurobrycon pteropus*, USNM 232921; *d, Xenurobrycon macropus*, USNM 219381; *e, Xenurobrycon heterodon*, USNM 219390.

We have not found a cordlike ligament in nonxenurobryconin glandulocaudines, although some other glandulocaudine males have strong skin and underlying connective tissue attaching a pouch scale or scales (not a lateral-line scale) to several adjacent fin rays of the ventral caudal-fin lobe (most often to fin rays 13 to 18, never to fin ray 10). Other characids and glandulocaudines may have relatively weak connective tissue fibers attaching the terminal lateral-line scale to rays 10 and 11, but this tissue never forms organized ligamentous tissue.

5. In sexually mature males the proximal tips of the medial two or three pelvic-fin rays project further anteriorly than the tip of the laterally adjacent ray (Figures 35, 36).

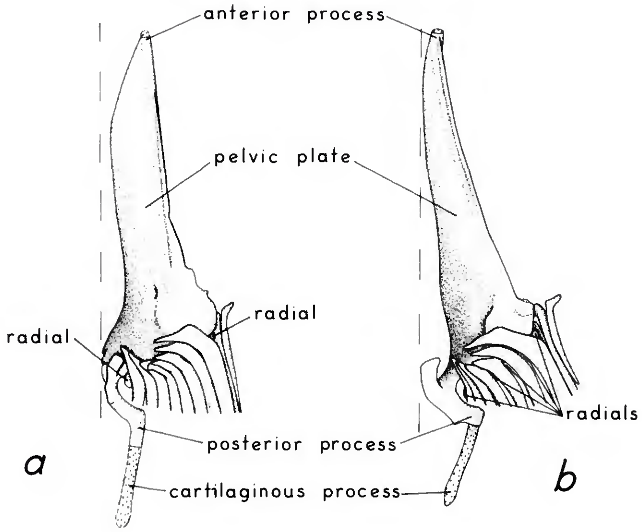
In other glandulocaudine and tetragonopterine characids the proximal tips of the medial two or three pelvic-fin rays do not extend as far anteriorly as the laterally adajacent ray (Figure 37*b*).

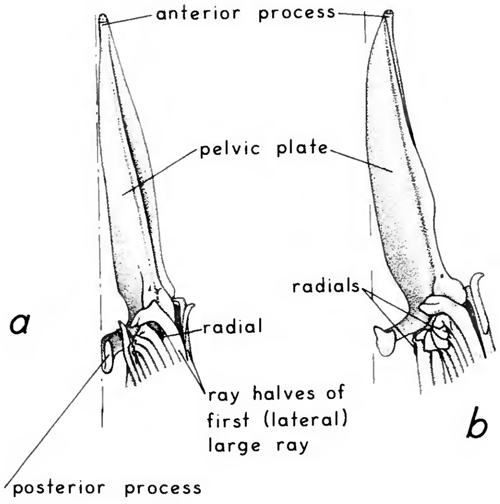
In *Xenurobrycon* (Figure 37*a*) this feature is not as obvious as in the others, in part because the proximal tips of all the rays are aligned in a shallow rather than a deep curve, and in part because of the unusual orientation of the girdle. In our view, however, the feature is still present; the condition in *Xenurobrycon* does not resemble the outgroup condition.

Genus *Argopleura* Eigenmann, 1913

Bryconamericus Eigenmann, 1913:10 [in part only].

Argopleura Eigenmann, 1913:10 [type-species *Bryconamericus magdalenensis* Eigenmann, 1913:14 by original designation in key; proposed as subgenus of *Bryconamericus* Eigenmann, McAtee, and Ward (1907:139)]; 1914:35 [included in a key to Glandulocaudinae]; 1922:147 [generic definition, placed in Tetragonopterinae]; 1927:395 [description, placed in Tetragonnopterinae next to *Bryconamericus*].—Myers in Eigenmann and Myers, 1929:467 [a note that *Argopleura* should be placed in the Glandulocaudinae].—Miles, 1943:54 [placed in Tetragonopterinae but thought it related to *Gephyrocharax* in Glandulocaudinae]; 1947:152 [placed in Tetragonopterinae but thought intermediate between Tetragonopterinae and





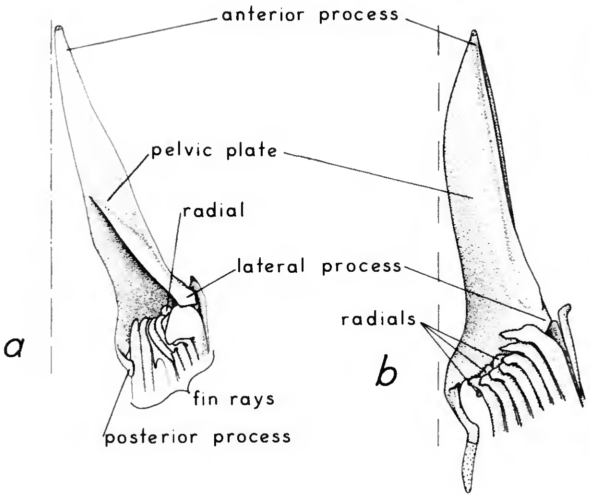


FIGURE 35 (top left).—Pelvic bone and proximal portion of pelvic-fin rays (ventral view, left side): *a, Argopleura chocoensis*, male, SL 45.5 mm, CAS 39030, Colombia, Choco, Río Juan, Istmina; *b, Iotabrycon praecox*, male, SL 17.7 mm, USNM 216802, Ecuador, Los Rios, Río Palenque.

FIGURE 36 (top right).—Pelvic bone and proximal portion of pelvic-fin rays (ventral view, left side): *a, Scopaeocharax atopodus*, male, SL 20.7 mm, USNM 207517, Peru, Huanuco, Río Huallaga, Tingo Maria; *b, Tyttocharax madeirae*, male, SL 15.6 mm, USNM 179540, Brazil, Amazonas, Rio Urubú.

FIGURE 37 (left).—Pelvic bone and proximal portion of pelvic-fin rays (ventral view, left side): *a, Xenurobrycon macropus*, male, SL 15.2 mm, USNM 219381, Paraguay, Paraguari, Lago Ypacarai; *b, Bryconamericus* sp., male, SL 80.6 mm, MCZ 48719, Ecuador, Los Rios, Arroyo Bambino, tributary to Río Cristal at Montalba.

Glandulocaudinae].—Böhlke, 1954:265 [comment on possible polyphyly of Glandulocaudinae in relation to *Argopleura*; p. 267, considered *Planaltina* closest to *Argopleura*]; 1958a:44 [*Argoplerua* coupled with *Planaltina* in key to Glandulocaudinae; Glandulocaudinae considered polyphyletic].—Nelson, 1964a:70 [noted sculpturing of caudal scale; p. 72, figure of tail of *Argopleura chocoensis* Eigenmann; p. 74, discussion of external caudal morphology; p. 80, geographical distribution and consideration as morphologically "generalized;" pp. 127–128, considered near *Bryconamericus*].—Géry, 1966:227 "considered *Gephyrocharax* possibly near *Argopleura*; p. 235, placed *Argopleura* and *Gephyrocharax* as a couplet in a key to Glandulocaudini].—Dahl, 1971:140 [placed in Tetragonopterinae].—Fowler, 1975a:28 [listed].—Géry, 1977:358 [placed *Argopleura* and *Gephyrocharax* as a couplet in a key to Glandulocaudini].

Aglopeura Travassos, 1951:16 [misspelling for *Argopleura*].

Xenurocharax Regan, 1913:463 [type-species *Xenurocharax spurrellii* Regan, 1913:463 by monotypy].—Eigenmann, 1927:395 [considered *Xenurocharax spurrelli* a synonym of *Argopleura chocoenis*].

Xemerocharax Travassos, 1952:140 [misspelling for *Xenurocharax*].

The above annotated synonymy and literature citations indicate that many authors believed *Argopleura* to be a relatively primitive glandulocaudine related in some way to *Bryconamericus* Eigenmann (in Eigenmann, McAtee and Ward, 1907:139). *Bryconamericus* is putatively a relatively unspecialized tetragonopterine group with species widely distributed in South America. Eigenmann (1913:10) described *Argopleura* as a subgenus of *Bryconamericus* and noted that males of *Argopleura* species had "lower caudal fulcra," which are absent in other species of *Bryconamericus*. Eigenmann related the species of *Argopleura* by "overall" similarity and listed no characters shared by them to the exlusion of all other characid genera. Subsequently Regan (1913:463) described *Xenurocharax*, a junior synonym of *Argopleura*, and more fully elucidated the caudal structures. He related *Xenurocharax* to *Deuterodon* Eigenmann (in Eigenmann, McAtee, and Ward, 1907:140), a characid genus not considered closely related to any glandulocaudine characids by subsequent authors (Eigenmann, 1927:341); Géry, 1977:519). We examined specimens of the type-species of the genus, *Deuterodon iguape* Eigenmann (MZUSP 18616), and found no evidence of glandulocaudine relationships. Eigenmann (1914:35) included *Argopleura* as a genus in a key to his newly established Glandulocaudinae but made no further comments about its relationships. Eigenmann (1927:395) placed *Argopleura* sequentially following *Bryconamericus* in his study of the American Characidae and considered it a "bridge between the Tetragonopterinae and the *Corynopominae*." Eigenmann here improperly used Corynopominae as a senior synonym of his Glandulocaudinae. Myers (in Eigenmann and Myers, 1929:467) noted that *Argopleura* is a glandulocaudine. Miles (1947:152) commented that *Argoplerua* is placed between the Tetragonopterinae and Glandulocaudinae because it has the dorsal fin in the middle of the body, a putative tetragonopterine character, and at the same time a "glandular scale" at the base of the central caudal-fin rays, a glandulocaudine character. Earlier, Miles (1943:54) stated that *Argopleura* shows some of the characters of *Gephyrocharax* of the Glandulocaudinae but listed no morphological similarities.

Böhlke (1954:265) considered *Argopleura* a glandulocaudine but noted the possible polyphyly of the Glandulocaudinae. Subsequently in the same paper (p. 267), he considered his new glandulocaudine genus, *Planaltina*, to be closest to *Argopleura* "in structural characters." However, he listed no morphological similarities, only differences between the two genera. Later, Böhlke (1958a:44) placed these two genera as a couplet in his key to the Glandulocaudinae. His key indicates that of all the glandulocaudine genera, only *Planaltina* and *Argopleura* share the character combination of the dorsal fin located nearer to the eye than to the caudal-fin base, males without hooks on the posterior anal-fin rays, and absence of a posterior anal-fin lobe. These are, however, all primitive glandulocaudine characters common also to the Tetragonopterinae as an outgroup and as such cannot be used to relate genera within the Glandulocaudinae. Furthermore, large adult males of some species of *Argopleura* have very small hooks as far posteriorly as principal anal-fin rays 21 and 22 (apomorphy 7).

Nelson (1964a:70) noted "the greatly enlarged and peculiarly sculptured [caudal] scale in *Argopleura*, *Tyttocharax*, and *Xenurobrycon*" but made no comment about a relationship among these genera. Nelson (1964a:127–128) considered *Argopleura* related to *Bryconamericus*, agreeing with the earlier opinions of Eigenmann (1913:10, 1927:395) and Böhlke (1954:267).

Géry (1966:227) thought *Gephyrocharax* possibly "near" *Argopleura* and on page 235 placed these two genera as a couplet in his key to the Glandulocaudini, based on a character, "Base of lower caudal lobe forming a distinct 'spur' in males." This description was apparently based on Eigenmann's statement (1913:10) that *Argopleura* species have "lower caudal fulcra" in males. The so-called lower caudal fulcra of males of most species of *Gephyrocharax* can be seen in the ventral caudal-fin lobe of *Gephyrocharax atricaudatus* (Figure 17). In that genus some of the procurrent ventral caudal-fin rays are modified, usually thickened, and somewhat separated from the more dorsal rays. A separation and less pronounced modification of these rays also occurs in *Corynopoma riisei* (Figure 16), as well as in the species of *Pterobrycon*. Not all species of *Gephyrocharax* have the ventral procurrent caudal-fin rays as highly modified as they are in *Gephyrocharax atricaudata*. Population samples of *Gephyrocharax venezuelae* Schultz show little to no modification except in a very few large, apparently old males. All *Argopleura* males that we examined lack such modifications and their ventral procurrent caudal-fin rays are like those of most characiforms. Compare these rays in *Argopleura* (Figures 8, 9) with those of *Landonia latidens* (Figure 18), *Phenacobrycon henni* (Figure 20), and *Brycon meeki* (Figure 21), fishes that never have been described as having a caudal spur or lower caudal fulcra.

Dahl (1971:140) placed *Argopleura* in the Tetragonopterinae without comment and Fowler (1975a:28) also placed *Argopleura* in the Tetragonopterinae without comment, apparently based on Eigenmann (1913:10).

Géry (1977:358) again placed *Argopleura* and *Gephyrocharax* as a pair in his key, this time based on the statement, erroneous for *Argopleura*, that most ventral procurrent caudal-fin rays in males of both genera are separated (dorsally) from the remainder of the fin. We find no separation in specimens of *Argopleura*. Géry said nothing further about possible relationships of *Argopleura* but noted that it shares some characters (unspecified) with *Bryconamericus*. The only characters we know these genera to share are primitive for the taxonomic levels just mentioned and are present in many other tetragonopterines. Thus these characters provide no information about a close genealogical relationship between these two genera.

Diagnosis.—The following two synapomorphies are diagnostic for *Argopleura* and corroborate a hypothesis that its known species are more closely related to one another than to any other species of xenurobryconin characids.

6. In sexually mature males the accessory pouch scale (defined under apomorphy 3) bears a posterodorsal process that extends medial to the pouch scale and is approximately rectangular in shape (shown by dashed lines in Figure 22). The joint border between the pouch scale and the accessory pouch scale is not a simple overlap. The borders are sinuous, thickened and form a squamosal joint. In addition, the posteroventral border of the accessory pouch scale forms the anterior part of the pouch opening (Figures 8, 9).

In a 37.0 and a 44.1 mm SL male of *Argopleura* sp. (ANSP 127516), the pouch scale and the accessory pouch scale were fused together, but such fusion is uncommon in this sample.

In all other male xenurobryconins the accessory pouch scale is of the usual characid scale shape with no posterodorsal process and its posterodorsal border lies lateral to the pouch scale rather than medial to it as in *Argopleura*. No other xenurobryconin, glandulocaudine, or characid known to us has a squamosal border between two caudal scales. This can be seen in *Iotabrycon praecox* (Figure 23), *Tyttocharax madeirae* (Figure 24), and *Xenurobrycon macropus* (Figure 25). Other glandulocaudines and characids sometimes have enlarged ventral lobe caudal-fin scales but never shaped like the accessory pouch scale of *Argopleura*.

7. The bony hooks [classified as contact organs by Collette (1977:226)] on the anal fin of sexually mature males occur in two major groups on the anterior half of the anal fin (Figure 38). In all specimens there was at least one, but usually two or three, hookless rays between the first and second groups of hooks. An anterior group of relatively small posterodorsally and laterally directed hooks occurs on the anterior 1–4 principal fin rays (the count starts with the longest anterior unbranched ray). Usually these hooks occur on principal rays 1–3, but in one sample of *Argopleura* sp. (USNM 220369) a very few and minute hooks were present only on principal rays 1 and 2. The second group, comprised of much larger, anterodorsally and laterally directed hooks, occurs approximately on principal rays 5–14, depending on the species. The hooks usually begin on ray 6 or 7 and terminate on rays 12 to 14. There are from one to four hooks per ray in the second group with two or three the most common numbers. A third group of posterodorsally directed hooks, distinguished by their very small size, may occur on the rays posterior to those bearing the second group. These hooks may be found on none to nearly all of the remaining posterior anal-fin rays.

The hooks on the anal-fin rays of other male xenurobryconins and glandulocaudines occur in a variety of forms and shapes, but not in two distinct groups. *Iotabrycon praecox* (Figure 39), *Scopaeocharax atopodus* (Figure 40), *Tyttocharax madeirae* (Figure 41), *Xenurobrycon macropus* (Figure 42), and *Xenurobrycon pteropus* (Figure 43) show some of this variety. Anal-fin hook placement in *Tyttocharax* could be interpreted as a terminal transition stage derived from the condition in *Argopleura*, but the most parsimonious cladogram contradicts this hypothesis. (See also apomorphy 67). Anal-fin hook placement in non-glandulocaudine characids can vary, but the hooks are most commonly located in the anterior third to half of the fin and are not reported to occur in two major groups. Wiley and Collette (1970:164), Roberts (1973:513), and Collette (1977:236–241) published accounts of hooks in characiform fishes. Fink and Weitzman (1974:11, 22) discuss seasonal variation in occurrence of anal-fin hooks of *Cheirodon affinis* (Meek and Hildebrand) (1916:275) and the lack of such variation in *Cheirodon dialepturus*. (See also the species description of *Xenurobrycon heterodon*, p. 89, concerning seasonal variation in hook presence.) We found no evidence of seasonal variation in *Argopleura*, but our sample was not large.

Subgroup A: *Iotabrycon, Xenurobrycon, Scopaeocharax,* and *Tyttocharax*

Synonymies and brief notes on the historical opinions about the putative relationships of these genera are presented under the treatment of each genus except *Scopaeocharax*. The species included in *Scopaeocharax, Tyttocharax*, and *Xenurobrycon* have been considered related by Böhlke (1958b). Roberts (1973) in describing *Iotabrycon* as new did not study its possible relationships with the xenurobryconin characids.

The following twelve synapomorphies corroborate a hypothesis that the genera of subgroup A are more closely related to one another than any of them is to another glandulocaudine or characid.

8. The pored lateral line is abbreviated or absent in

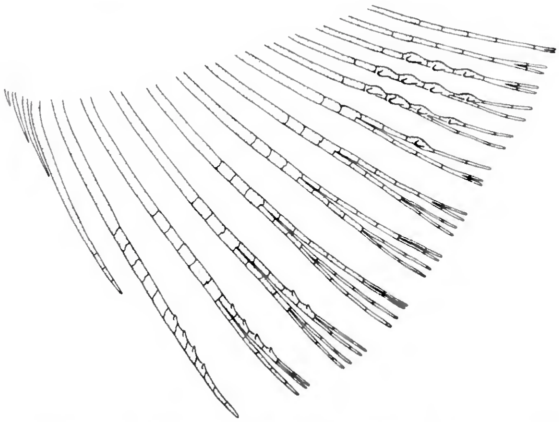


FIGURE 38.—*Argopleura chocoensis*, anterior anal-fin rays (lateral view, left side), male, paratype, SL 45.5 mm, CAS 39030, Colombia, Choco, Río San Juan, Istmina.

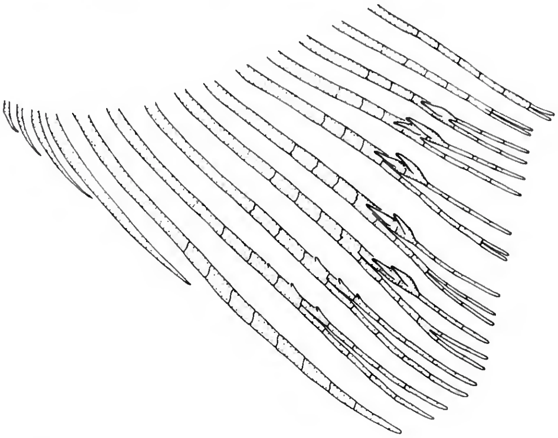


FIGURE 39.—*Iotabrycon praecox*, anterior anal-fin rays (lateral view, left side), male, SL 17.7 mm, USNM 210802, Ecuador, Los Rios, Río Palenque.

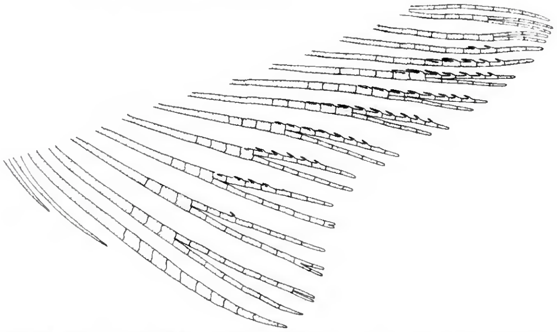


FIGURE 40.—*Scopaeocharax atopodus*, anal-fin rays (lateral view, left side), male, SL 20.7 mm, USNM 207517, Peru, Huanuco, Rio Huallaga, Tingo Maria.

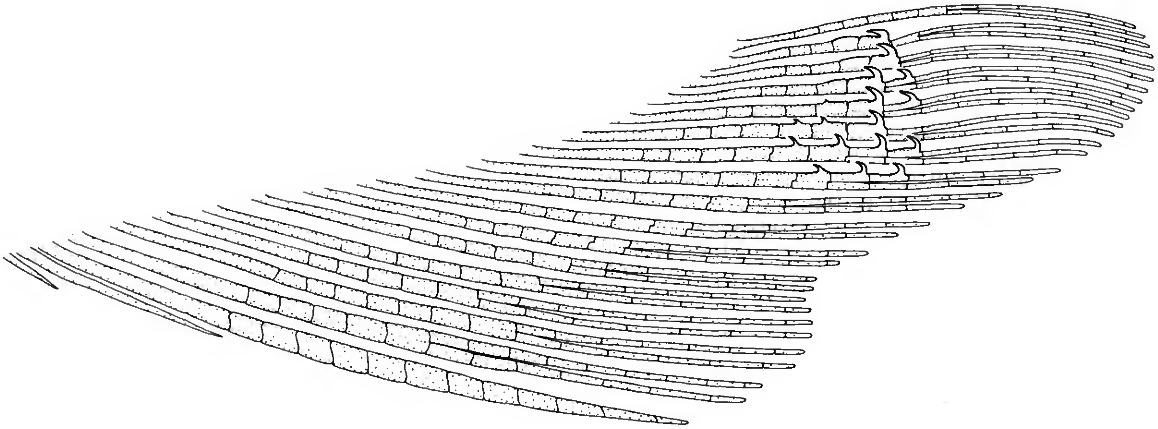


FIGURE 41.—*Tyttocharax madeirae*, anal-fin rays (lateral view, left side), male, SL 15.6 mm, USNM 179540, Brazil, Amazonas, Rio Urubú.

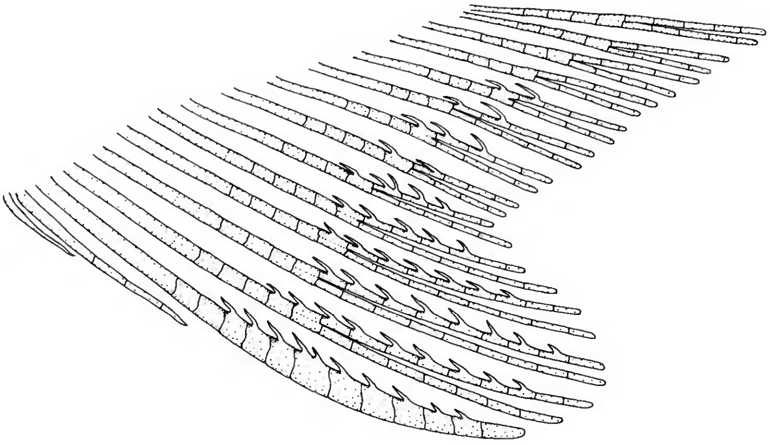


FIGURE 42.—*Xenurobrycon macropus*, anal-fin rays (lateral view, left side), male, SL 14.4, USNM 219381, Paraguay, Paraguari, Lago Ypacarai.

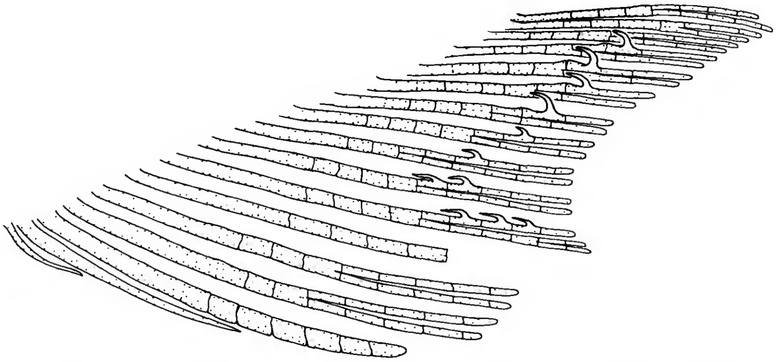


FIGURE 43.—*Xenurobrycon pteropus*, anal-fin rays (lateral view, left side), male, SL 13.8 mm, paratype, USNM 232921, Brazil, Amazonas, Fonte Boa.

adults of both sexes, perforating from zero to seven anterior scales, and the pouch scale of sexually mature and maturing males lacks a laterosensory canal (Figures 23–32).

Species of *Argopleura* have a complete lateral-line system that includes a tube in the pouch scale (Figure 22). (See also apomorphy 3.) Most other glandulocaudines also have a complete lateral line. *Glandulocauda* and *Mimagoniates* (Figure 19) have an incomplete lateral line but no other xenurobryconin synapomorphies. Therefore we consider their abbreviated lateral-line canal system to be independently evolved.

All xenurobryconins of subgroup A are small fishes. Many other small to minute characiforms of various lineages demonstrate such an absence or reduction in the canals of the laterosensory system. The laterosensory canal system in miniature fishes may be so small that the effectiveness of the neuromasts and associated cupulae as stimulus receptors in a laterosensory canal is reduced due to increased resistance of water to flow associated with the boundary layer effect in small tubes (Leyton, 1975:5). The neuromasts and accompanying cupulae may be on the body surface as in many larval fishes (Iwai, 1967). We were unable to locate neuromasts in these fishes with the techniques used in this study. It may also be that the lack of canals and their associated bony structures is primarily a function of the small size of these fishes at maturity and the truncated developmental time required to reach that maturity and size. Whatever the association may be, most adult characins, which reach only 12 to 25 millimeters in standard length at maturity, have reduced laterosensory canal and pore components of their laterosensory system. (See discussion, p. 97, of caudal pump alterations associated with small tube size. See also Weitzman and Fink, 1983:345, for a discussion of systematic significance of laterosensory reduction.) According to the most parsimonious consideration of character distribution among characid taxa, this character has evolved independently in this group.

9. In sexually mature males the posteroventral muscle slip comprised of the lateralis superficialis and hypaxialis muscles does not insert on principal caudal-fin rays 15 to 17 (Figures 44–47).

Other glandulocaudines and characids examined have a tendinous insertion from these muscles to principal caudal-fin rays 15 to 17 (Figures 48, 49).

10. In sexually mature males the posterodorsal muscle slip comprised of lateralis superficialis and the separate, posterior epaxialis muscles does not insert on principal caudal-fin ray 4 (Figures 44–47).

The other glandulocaudines and characids examined have tendinous insertions from this muscle group to the fourth principal caudal-fin ray (Figures 48, 49).

11. In sexually mature males the ossified posterior portion of the posterior pelvic process is reduced relative to its form in other glandulocaudines and most other characids (Figures 35*a*,*b*, 37*a*).

The longer posterior ossification of most other characids is evident in *Argopleura* and *Bryconamericus* (Figures 35*a* and 37*b*, respectively).

Gasteropelecine characids lack a posterior ossified process (Weitzman, 1954:260, fig. 18), but this reduction is hypothesized to have evolved independently in that taxon on the basis of the most parsimonious consideration of all characters and taxa involved.

12. The pelvic bone of adult males is located so that from lateral view its anterior tip lies between or slightly anterior to the ventral tips of the anterior two pleural ribs (ribs of the fifth and sixth vertebrae).

In other characids the anterior tip of the pelvic bone lies in the region ventral to the tips of the second to third pleural ribs (ribs of vertebrae 6 and 7). The same is true of other glandulocaudines, except *Corynopoma* in which it is ventral to the tip of the first rib (vertebra 5) and *Pterobrycon* in which it extends anteriorly to the first postcleithrum. In *Corynopoma* the position of the pelvic bone is not sexually dimorphic. The most parsimonious consideration of characters and taxa indicates that the position of the anterior pelvic-bone tip in *Corynopoma* and *Pterobrycon* is a homoplasy relative to the position in xenurobryconin subgroup A. (See also apomorphies 41, 42, 53, 62).

13. In adults of both sexes the posteromedial (parietal) branch of the supraorbital (frontal) sensory canal is reduced

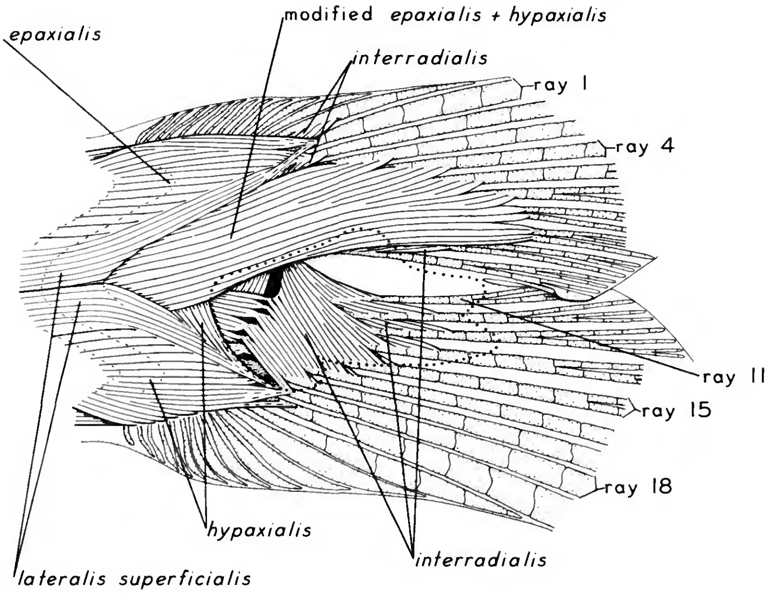


FIGURE 44.—*Iotabrycon praecox*, superficial caudal musculature (lateral view, left side), male, composite based on 2 specimens, SL 12.6 and 13.1 mm, MCZ 50602, Ecuador, Los Rios, Río Palenque. Border of pouch scale shown in heavy dotted line.

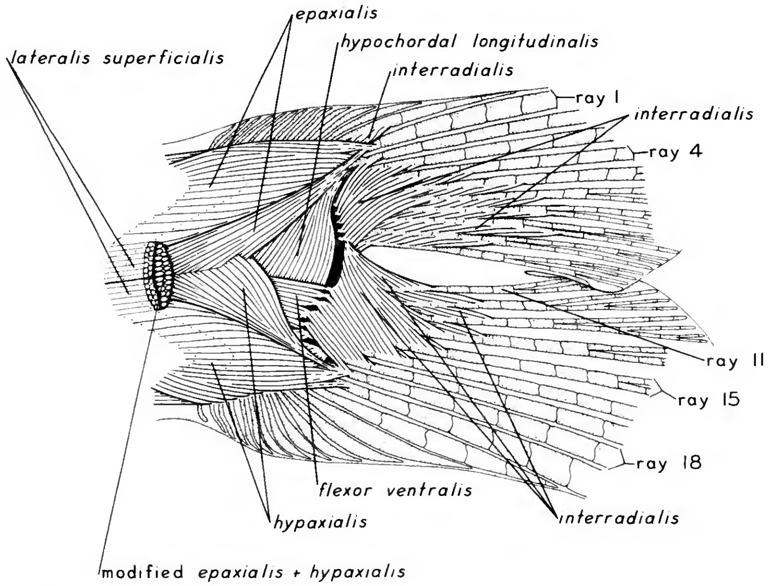


FIGURE 45.—*Iotabrycon praecox*, caudal musculature (lateral view, left side), male, composite based on 2 specimens, SL 12.6 and 13.1 mm, MCZ 50602, Ecuador, Los Rios, Río Palenque. Lateralis superficialis and most of modified epaxialis + hypaxialis muscle bundle removed, revealing interradialis muscles of dorsal caudal-fin lobe and other underlying muscles.

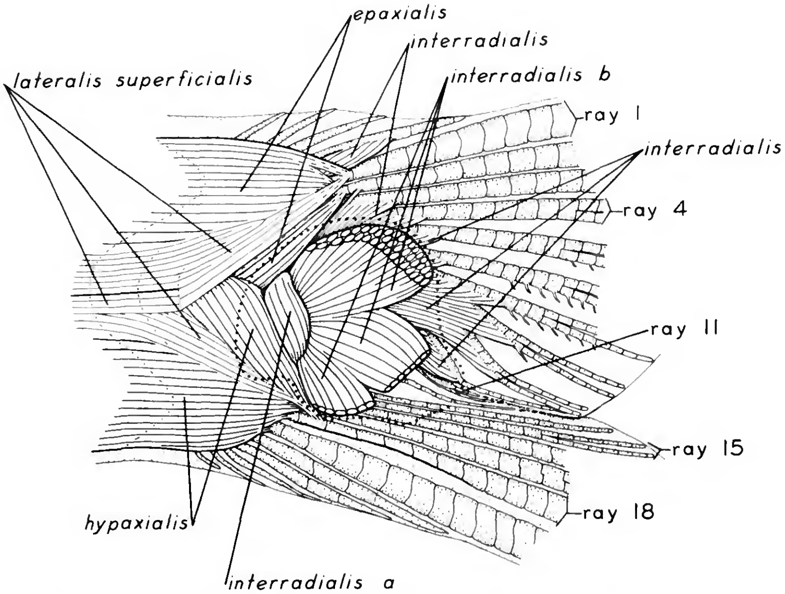


FIGURE 46.—*Scopaeocharax atopodus.* caudal musculature (lateral view, left side), male, SL 21.3 mm, USNM 207517, Peru, Huanuco, Río Huallaga, Tingo Maria. Border of pouch scale represented by heavy dotted line. Three divisions of fan-shaped interradialis-b muscle shown with cut borders near where they insert on medial face of pouch scale.

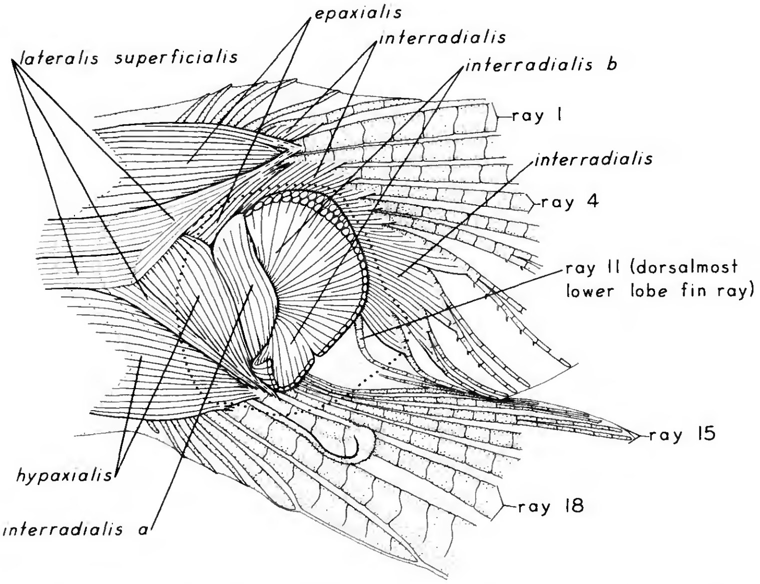


FIGURE 47.—*Xenurobrycon macropus*, caudal musculature (lateral view, left side), male, SL 15.4 mm, USNM 219381, Paraguay, Paraguari, Lago Ypacarai. Border of pouch scale represented by heavy dotted line. Fan-shaped interradialis-b muscle illustrated with cut borders near where it inserts on medial face of pouch scale. Anteroventral corner of interradialis-b pulled up to reveal insertions of hypaxialis and lateralis superficialis muscle slips.

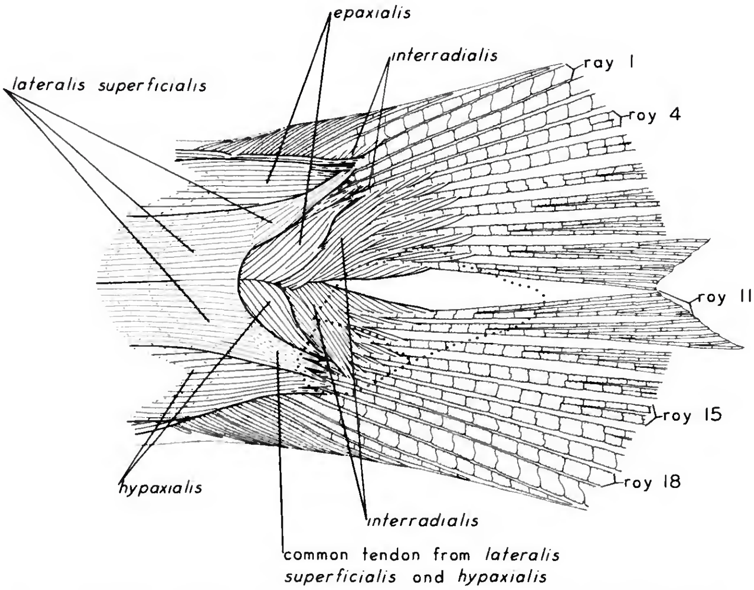


FIGURE 48.—*Argopleura chocoensis*, caudal musculature (lateral view, left side), male, SL 46.3 mm, paratype, USNM 76943, Colombia, Choco, Río San Juan, Istmina. Lateral, visible borders of 2 large scales shown in heavy dotted line.

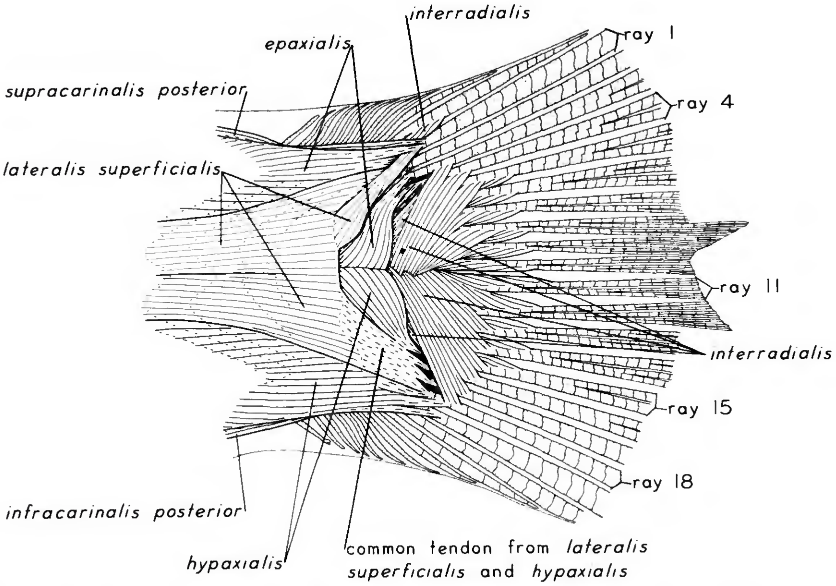


FIGURE 49.—*Bryconamericus* sp., caudal musculature Lateral view, right side, reversed so as to appear as left side), male, SL 75.5 mm, MCZ 48719, Ecuador, Los Rios, Arroyo Bambino, tributary of Río Cristal at Montalba.

in length, never extending into the parietal bone (Figures 50–55).

Argopleura (Figure 56), all other glandulocaudines, and most large characids (longer than about 30 mm SL as adults) (Figures 57, 58) have the posteromedial branch of the supraorbital canal extending almost to the posterior margin of the parietal bone. (See apomorphy 8 and Weitzman and Fink, 1983:391–394, for further comments on small size and laterosensory canal reduction in characids.)

14. The laterosensory canal of the posttemporal bone of adults of both sexes is absent (Figures 51–55).

In *Argopleura* (Figure 56), other glandulocaudines, and most characids (Figures 57, 58) a laterosensory canal is present in the posttemporal. In *Argopleura* sp. (Figure 56), the posttemporal canal is partly obscured by the extrascapular superficial to it.

15. The anteroventral limb or process of the posttemporal bone is unossified in both sexes, and the ligament that typically extends between this process and the skull in most characids attaches to the ventral region of the posttemporal bone.

The anteroventral posttemporal limb is present in all other glandulocaudines and most other characids examined, and is well developed in *Argopleura*. The ossification of the anteroventral limb is reduced and sometimes absent (although the ligament remains) in a variety of usually small species of characids that have several other skull reductions. *Paracheirodon* is a typical example of miniature characids in which this limb is reduced (Weitzman and Fink, 1983, figs. 6–8); compare with their illustration of *Gymnocorymbus* (1983, fig. 10) in which the posttemporal is complete. We hypothesize that absence of this process in subgroup A is independent of its loss or reduction in other small to minute characids.

16. In adults of both sexes some teeth of the premaxilla form one or more diagonal series oriented from lateral to slightly anterodorsal (Figures 59–65).

In other glandulocaudines and in most tetragonopterine characids, the teeth on the premaxillae are aligned in two approximately even rows along the ventral border of the bone (Figure 66). Small characids and a few large characids have teeth in a wide variety of forms and shapes, but we know of none with a tooth arrangement like any of those illustrated here for xenurobryconin subgroup A.

There is a considerable amount of variation in the upper jaw teeth of subgroup A, from simple conic teeth as in *Iotabrycon praecox* (Figure 59), to partly bicuspid and tricuspid as in some specimens of *Xenurobrycon heterodon*, to the conic-toothed, "burr mouths" of *Tyttocharax madeirae* (Figure 62). Inspection shows that all these fishes have one or more diagonal series.

17. All jaw teeth are conical in adults of both sexes (Figures 59–64). *Xenurobrycon heterodon* (Figure 65) is an exception, having some teeth bi- or tricuspid in the dentary and also sometimes in the premaxilla. The possession of multicuspid teeth in this species is most parsimoniously explained as an autapomorphous reversal.

In *Argopleura* (Figure 66), other glandulocaudines, and most other "tetragonopterines," all jaw teeth are multicuspid in adults. (See Weitzman and Fink, 1983), for discussions of the of tooth cusp number and phylogeny in American characids.) Some other characid groups, for example the Characinae as defined by Géry (1977:295, 302), have conical teeth. The presence of conical teeth in subgroup A xenurobryconins and in some other characid groups is hypothesized to be a convergence.

18. Adult size is small, not known to reach a standard length exceeding 25 mm. The mean standard length of all the largest specimens examined for all species in the subgroup was 19.2 mm.

All other glandulocaudines, except *Pterobrycon landoni*, are known to have adults exceeding 30 mm standard length. The largest specimen of each of the 36 species of nonxenurobryconin glandulocaudines examined range from 25.1 to about 100.0 mm standard length with a mean of 46.9 mm. All species of *Argopleura* examined had adults exceeding 44.0 mm standard length, the largest being 52.8 mm standard length for *Argopleura chocoensis*.

Pterobrycon landoni is known only from the

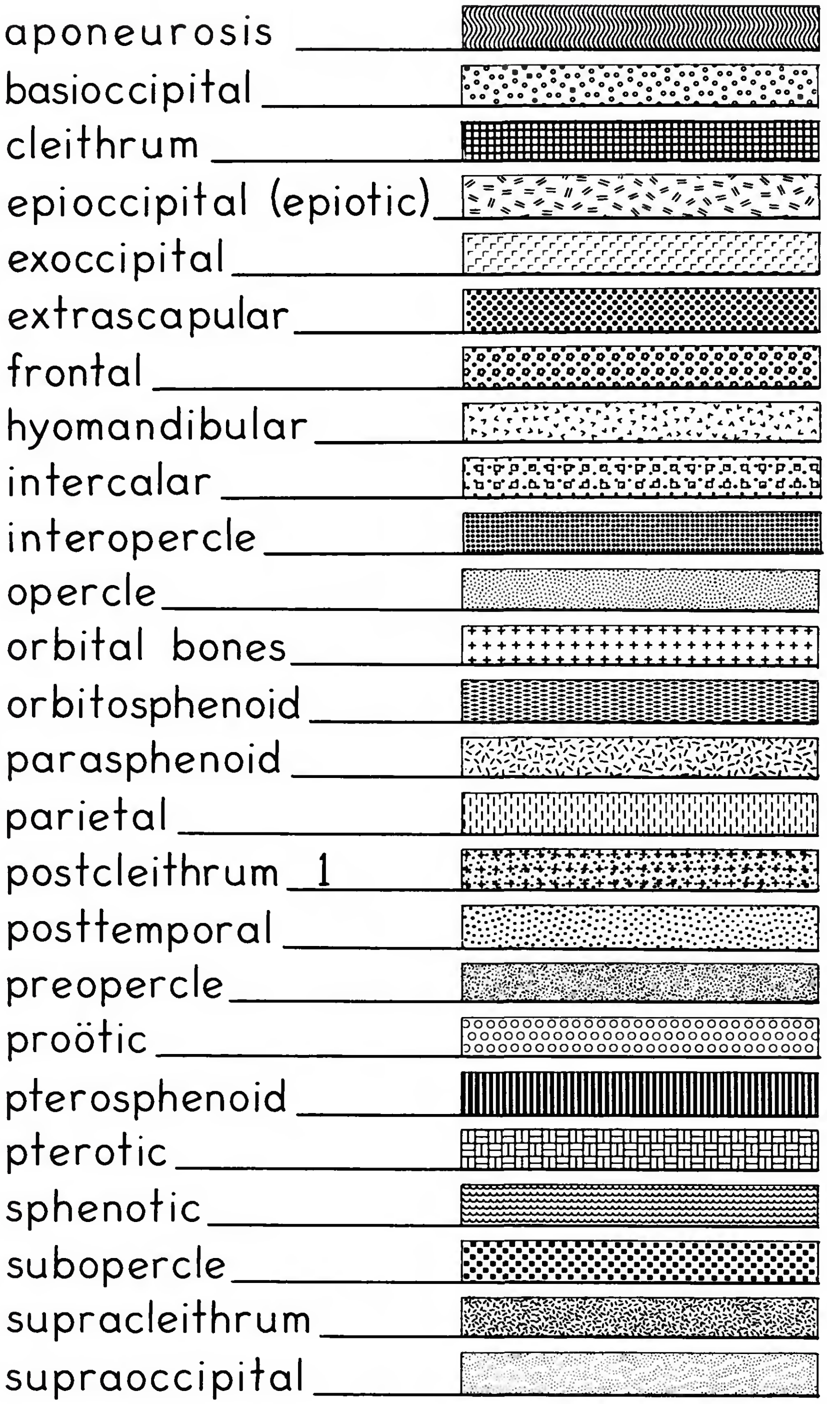


FIGURE 50.—Guide to graphic representation of skull and shoulder girdle bones.

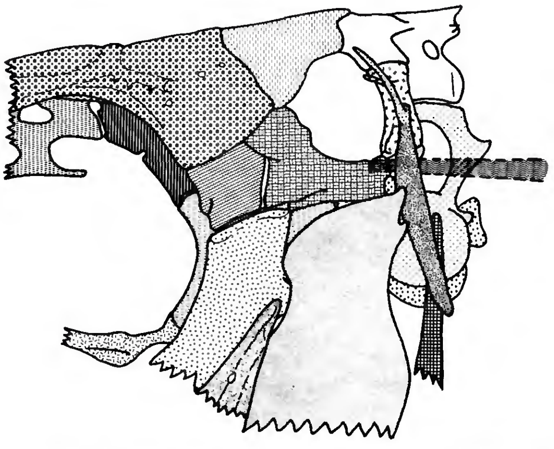


Figure 51.—*Iotabrycon praecox*, posterodorsal region of skull, pectoral girdle with pterotic aponeurosis (lateral view, left side), male, SL 17.7 mm, USNM 216802, Ecuador, Los Rios, Río Palenque. Note: In this specimen cleithrum and supracleithrum are fused together.

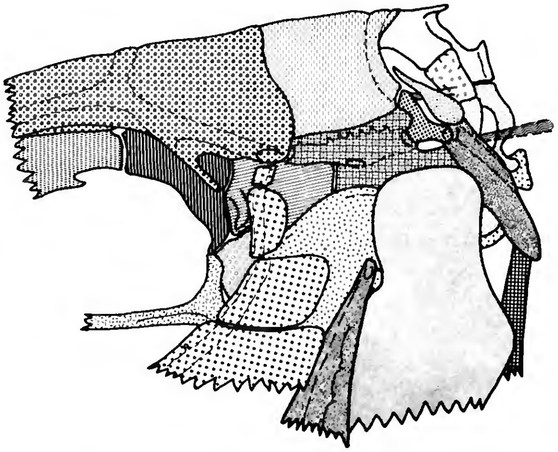


Figure 53.—*Scopaeocharax rhinodus*, posterodorsal region of skull, pectoral girdle with pterotic aponeurosis (lateral view, left side), male, SL 20.8 mm, paratype, ANSP 78711, Peru, Huanuco, Río Rondos, tributary of Río Monzon, Tingo Maria.

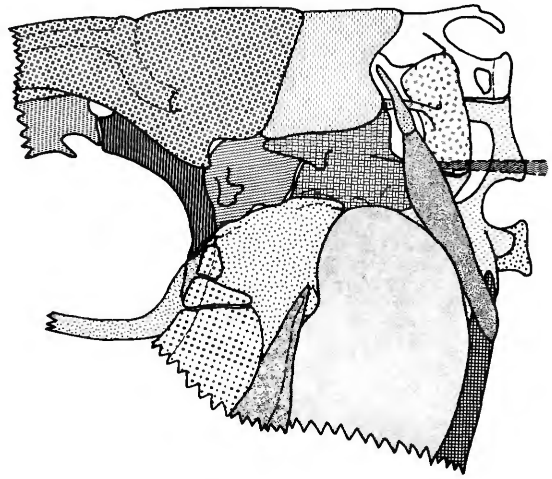


Figure 52.—*Scopaeocharax atopodus*, posterodorsal region of skull, pectoral girdle with pterotic aponeurosis (Lateral view, left side), male, SL 21.1 mm, USNM 207517, Peru, Huanuco, Río Huallaga, Tingo Maria.

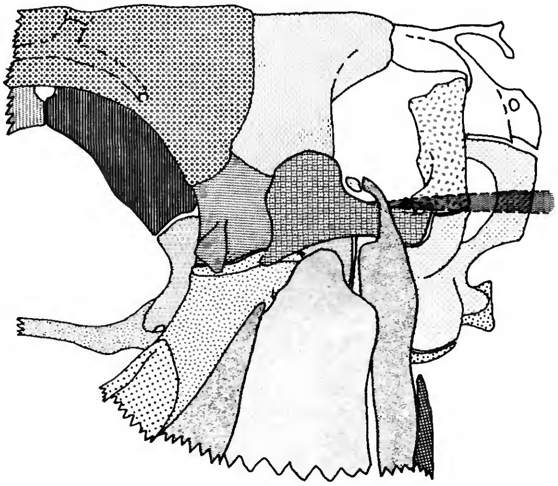
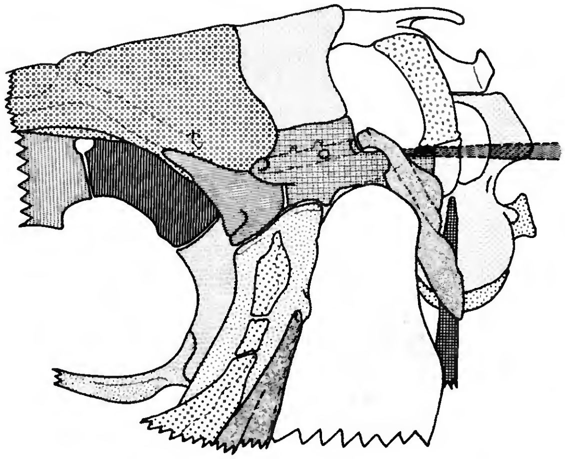


Figure 54.—*Tyttocharax madeirae*, posterodorsal region of skull, pectoral girdle with pterotic aponeurosis (lateral view, left side), male, SL 17.9 mm, USNM 179540, Brazil, Amazonas, Rio Urubú.

holotype, a mature male 25.1 mm standard length. This indicates that small size may have evolved independently in this species. However, there is no reason to believe that *P. landoni* get no larger. Some males of *Pterobrycon myrnae* often mature at about 25.0 mm standard length but others, which mature late, will exceed 30.0 mm standard length. *Pterobrycon landoni* may get much larger than the one known individual indicates. In a related species, *Corynopoma riisei*, males will often mature at about four months of age and 24.0 mm standard length. Other individ-



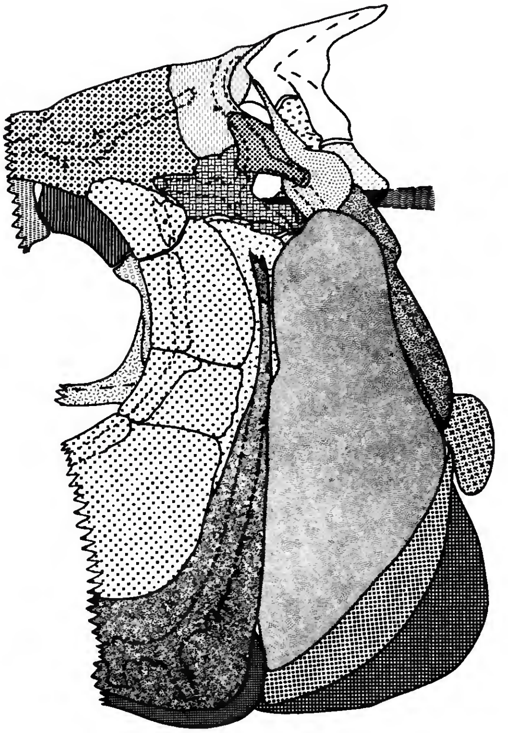
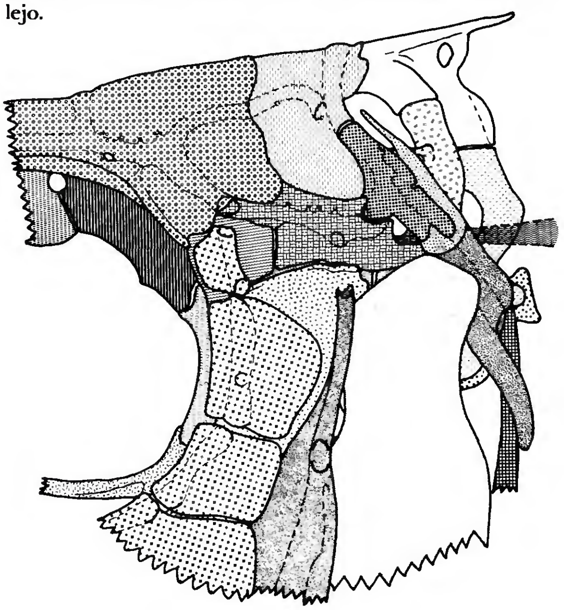


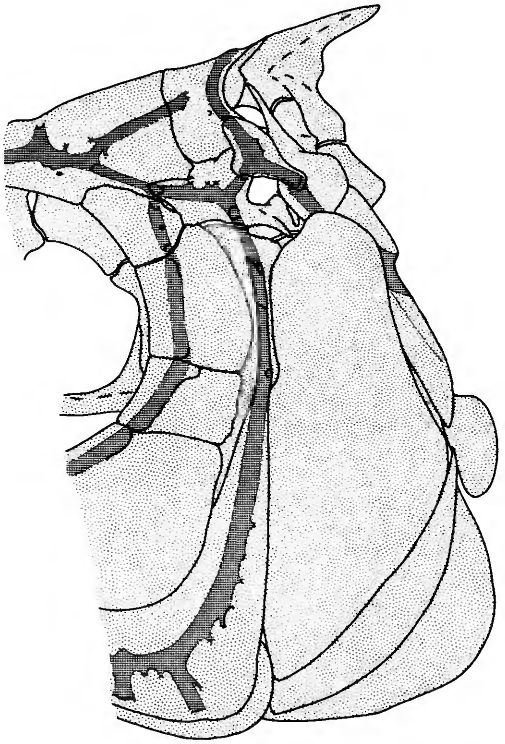
FIGURE 55 (top left).—*Xenurobrycon heterodon*, posterodorsal region of skull, pectoral girdle with pterotic aponeurosis (lateral view, left side), male, SL 16.4 mm, USNM 219390, Ecuador, Pastaza, Río Bobonaza.

FIGURE 56 (bottom left).—*Argopleura* sp., posterodorsal region of skull, pectoral girdle with pterotic aponeurosis (lateral view, left side), male, SL 42.3 mm, ANSP 127515, Colombia, Caldas, Río Mercedes.

FIGURE 57 (top right).—*Astyanax mexicanus*, posterior region of skull, pectoral girdle with pterotic aponeurosis (lateral view, left side), female, SL 52.4 mm, MCZ 41365, Mexico, Tamaulipas, Río Guaylejo.

FIGURE 58 (bottom right).—*Astyanax mexicanus*, posterior region of skull, pectoral girdle (lateral view, left side), female, SL 52.4 mm, MCZ 41365, Mexico, Tamaulipas, Río Guaylejo.





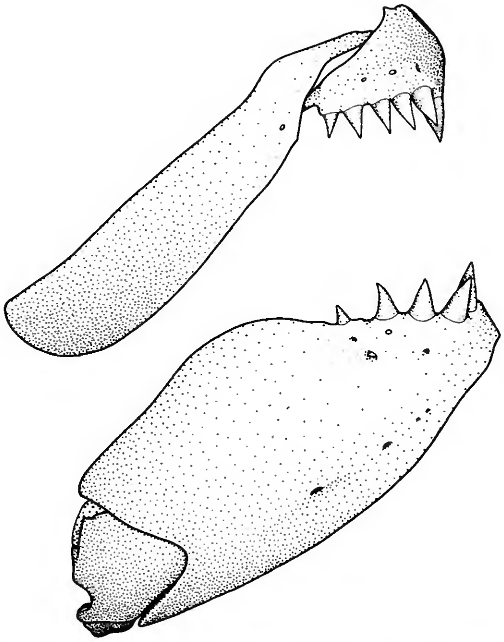


Figure 59.—*Iotabrycon praecox*, jaws and dentition (anterolateral view, right side), male, SL 21.5 mm, USNM 216802, Ecuador, Los Rios, Río Palenque.

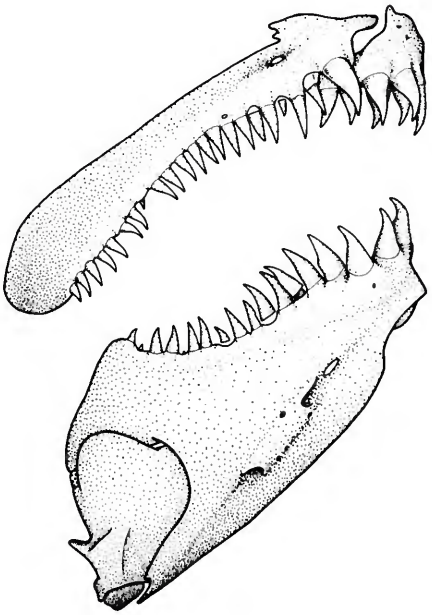


Figure 60.—*Scopaecharax atopodus*, jaws and dentition (lateral view, right side), male, SL 21.1 mm, USNM 207517, Peru, Huanuco, Río Huallaga, Tingo Maria.

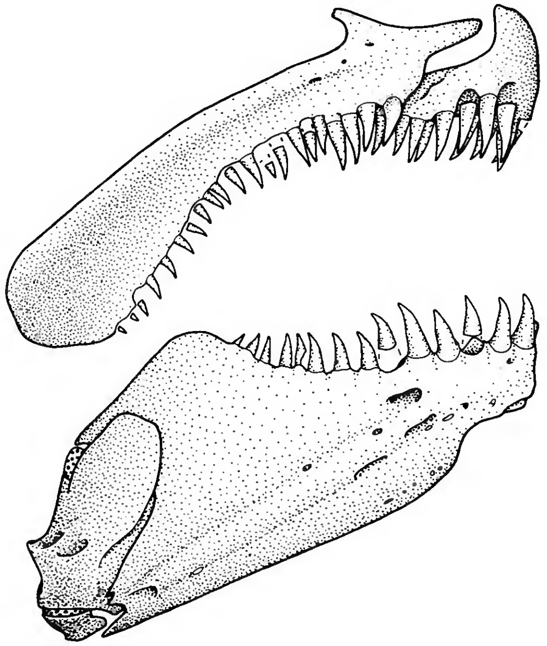


Figure 61.—*Scopaeocharax rhinodus*, jaws and dentition (anterolateral view, right side), male, SL 20.7 mm, paratype ANSP 78711, Peru, Huanuco, Río Rondos, tributary of Río Monzon, vicinity of Tingo Maria.

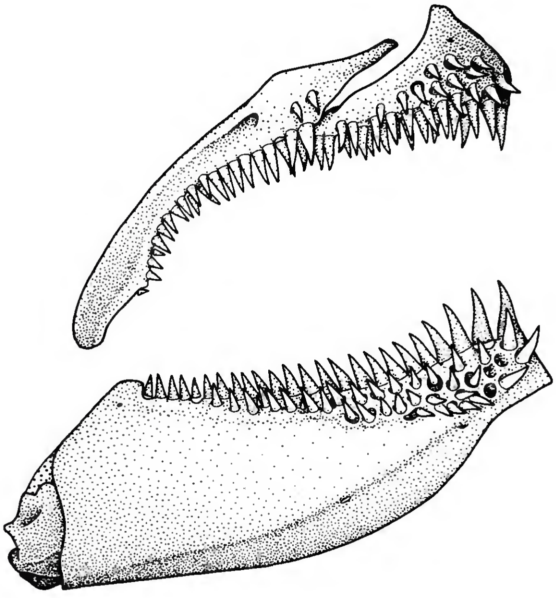


Figure 62.—*Tyttocharax madeirae*, jaws and dentition (anterolateral view), male, SL 15.4 mm, USNM 179540, Brazil. Amazonas, Rio Urubú.

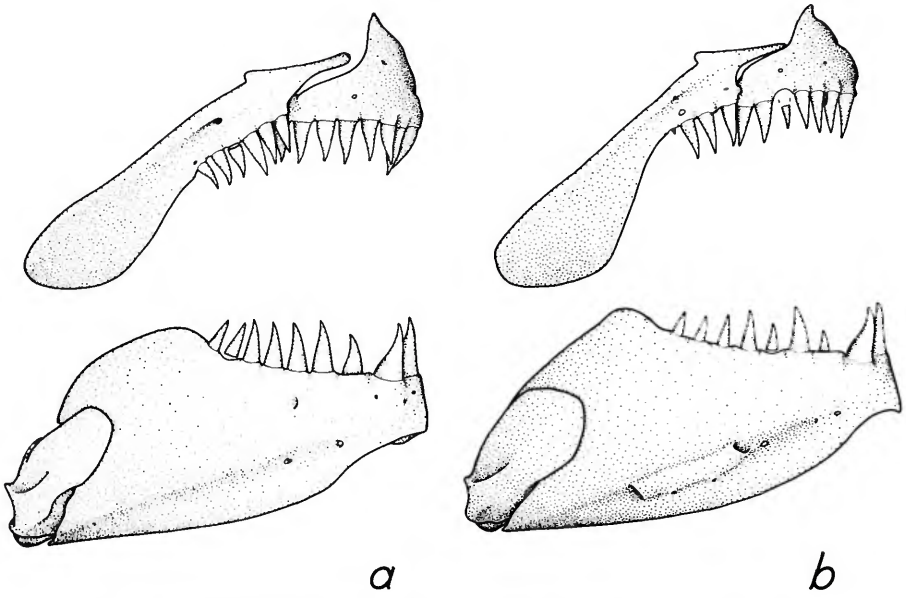


FIGURE 63.—*Xenurobrycon macropus,* jaws and dentition (anterolateral view, right side): *a,* male, SL 16.3 mm, paratype, CAS 40764, Brazil, Mato Grosso, Rio Bodoquena; *b,* male, SL 14.4 mm, USNM 219381, Paraguay, Paraguari, Lago Ypacarai.

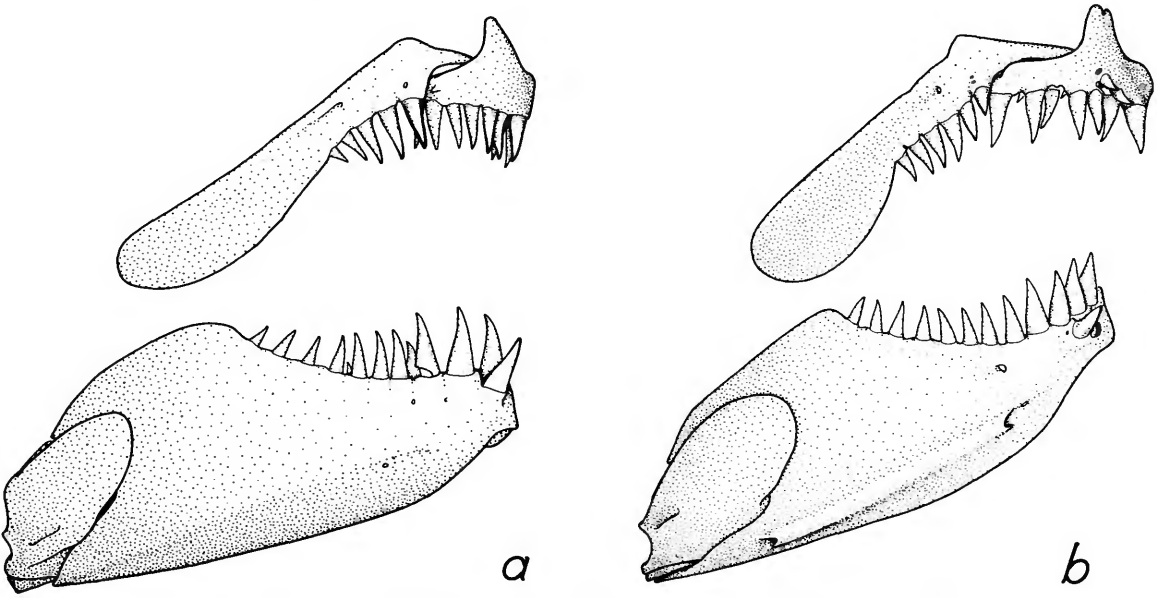


FIGURE 64.—Jaws and dentition (anterolateral view, right side): *a, Xenurobrycon macropus,* female, SL 15.6 mm, UMMZ 205484, Paraguay, Central, 7 km E of Luque on road to Aregua; *b, Xenurobrycon pteropus,* male, SL 13.8 mm, paratype, USNM 232921, Brazil, Amazonas, Fonte Boa.

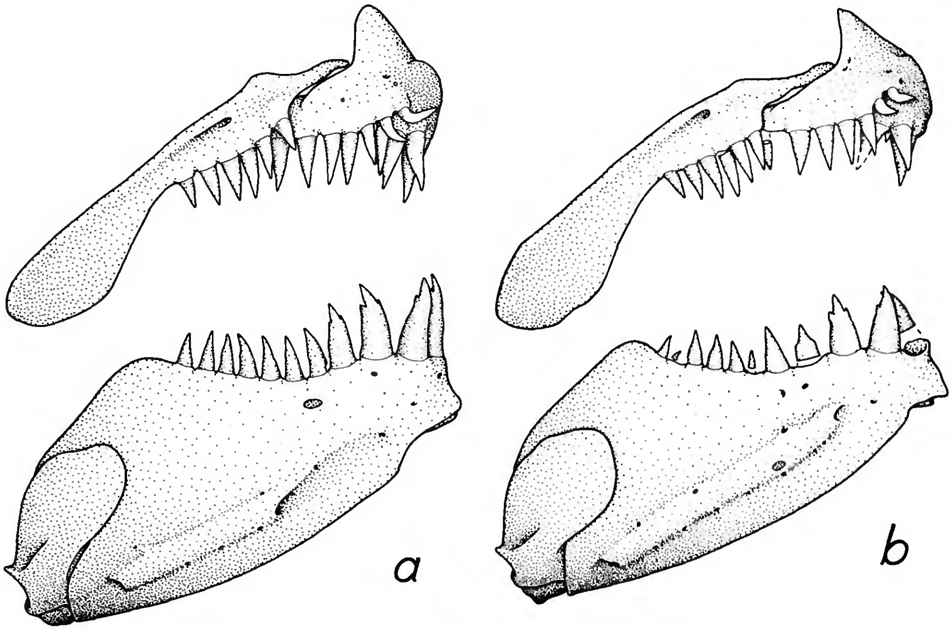


FIGURE 65.—*Xenurobrycon heterodon,* jaws and dentition (anterolateral view, right side): *a,* male, SL 16.7 mm, paratype, USNM 219391, Peru, Huanuco, Río Pachitea; *b,* male, SL 16.4 mm, paratype, USNM 219390, Ecuador, Pastaza, Río Bobonaza.

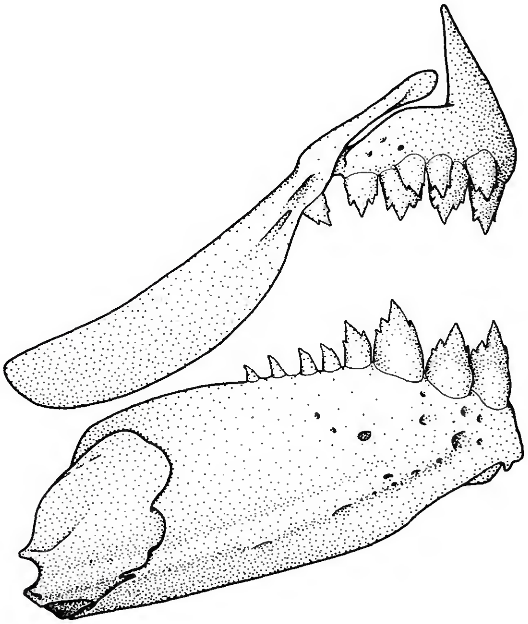


FIGURE 66.—*Argopleura chocoensis,* jaws and dentition (anterolateral view, right side), male, SL 45.5 mm, paratype, CAS 39030, Colombia, Choco, Río San Juan, Istmina.

uals, maturing a few months later, will be over 36.0 mm standard length. Early and late maturation and variation in size of adult males is common in *Corynopoma,* both in aquarium specimens raised from the same parents and in wild populations. Delayed maturation or at least variation in size of maturing males may be common in more than one glandulocaudine group. For example, the wild-caught sexually mature male *Xenurobrycon macropus* used in the illustration of the developed scale (Figure 28) is smaller than the wild-caught male used to draw the developing scale (Figure 31). (See pp. 32 and 62, for further discussions on small size in characids.)

Genus *Iotabrycon* Roberts, 1973

Iotabrycon Roberts, 1973:491 [type-species: *Iotabrycon praecox* Roberts, 1973:492 by original designation].—Géry, 1977:359 [listed in key].—Mahnert and Géry, 1984:510 [note on caudal skeleton].

Roberts (1973) in his original description of *Iotabrycon praecox* hypothesized and investigated the relationships of *Phenacobrycon*, *Landonia*, and *Iotabrycon*, all, so far as is known, monotypic and endemic to the Guayas basin in western Ecuador. We examine this hypothesis in the discussion section, pp. 62–64. Roberts found no specialized characters shared only by these taxa.

Géry (1977:359) keyed *Iotabrycon praecox* to a couplet including *Landonia latidens* and stated that *Iotabrycon* was "of uncertain lineage, possibly close to the Aphyoditeina." This is an assemblage of minute nonglandulocaudine characids discussed by Géry (1973) and we doubt its monophyly. Géry (1977:359) presented no evidence for this suggested relationship, but we infer that Géry was considering the small size of *Iotabrycon* and its possession of few and conic teeth. See Géry (1973:81) for a definition of the Aphyoditeina.

Roberts (1973:491) described a number of putative diagnostic characters for *Iotabrycon*, a few of which appear to be autapomorphies and therefore distinguish *Iotabrycon* from its relatives. Most of the "diagnostic" characters used by Roberts are descriptive but not by themselves diagnostic although they may be diagnostic in combination. These characters are primitive for either characids, glandulocaudines, xenurobryconins, or xenurobryconin subgroup A. Some are of uncertain polarity or homoplasies present also in some members of xenurobryconin subgroup B and are not included below.

DIAGNOSIS.—The following ten features are diagnostic for *Iotabrycon* and are autapomorphies of *Iotabrycon praecox*.

19. The parhypural and hypural 1 are fused together in females as well as in males.

In all other xenurobryconins such fusion is present only in males. (See apomorphy 1 for further discussion.)

20. In adult males the distal tips of the adjacent, median branches of principal caudal-fin rays 10 and 11 are enlarged in the sagittal plane and have rounded bladelike borders, which face each other (Figure 10).

Enlarged bladelike distal fin-ray segments are not present in other glandulocaudines or characids. In males of some species of *Argopleura* (Figure 9), the median branches of rays 10 and 11 have several short, median branches which together form a spatulate effect somewhat similar to that of the bladelike segments in *Iotabrycon*. Based on the differences in morphology this superficial similarity is judged not homologous.

21. The ventral region of the pouch scale of sexually mature males is posteriorly lengthened, consisting of hypertrophied, long accessory bony fimbriae (Figures 10, 23). As a result of the hypertrophy of this region, the accessory pouch scale is separated from the opening of the caudal sac since the opening is bordered ventrally by the elongate accessory bony fimbriae.

A similar fimbriate process is absent in scales of other xenurobryconins and most other glandulocaudines. The large caudal-fin scale in males of both species of *Pseudocorynopoma* and of *Hysteronotus megalostomus* has an elongate, ventrally located slender posterior process. However, since the pouch scale in these fishes is not derived from the posterior terminal lateral-line scale, we hypothesize that the process in these genera is not homologous with that in *Iotabrycon*.

Roberts (1973:494, fig. 3) illustrated and discussed one of the posterior series of fimbriae as detached from the ventral posterior process. Roberts stated that this series of fimbriae might represent a separate scale, although he indicated this hypothesis to be questionable. All specimens we have seen, incuding those examined by Roberts, have no detached fimbriae. We found that it requires twisting and turning of the scale in various lights to ascertain this. This manipulation is especially necessary in the specimen drawn by Roberts.

22. The posterior epaxialis and hypaxialis muscles of adult males have a large modified combined bundle or mass, which extends from the lateral midline of the caudal peduncle just deep to the lateralis superficialis and inserts distally on principal caudal-fin rays 3–8 superficial to and at the point of the posterior insertions of the interradialis muscles (Figure 44).

In other glandulocaudines and characids and in female specimens of *Iotabrycon* the epaxialis inserts on the bases of the dorsal principal rays 2–5, anterior to the posterior insertions of the interradialis bundles. The hypaxialis inserts only on ventral caudal-fin lobe rays and the epaxialis and hypaxialis muscle bundles are always separated by a connective-tissue septum (Figures 46–49).

23. The interradialis muscles of sexually mature males have the following special features: The fibers extending from the midbase of the caudal fin to principal fin-ray 10 are very restricted in length, attaching only near the base of ray 10. The fibers that extend across adjacent rays, rather than between adjacent rays, are much less extensive in the dorsal caudal-fin lobe than in the ventral lobe, and the dorsalmost proximal attachment of the fibers of the ventral caudal-fin lobe is to principal ray 10 (Figures 44, 45).

In other glandulocaudines and characids the muscle bundles from the midbase of the caudal fin to principal ray 10 are at least as extensive as those from the middle of the fin to ray 11; the fibers extending across adjacent rays are at least as extensive in the dorsal lobe as in the ventral lobe; and the dorsalmost proximal attachment of the ventral-lobe muscle bundles is either principal ray 11 (Figures 46, 47) or a septum extending across the middle of the caudal peduncle.

24. The predorsal region lacks scales in adults of both sexes.

We know of no other glandulocaudines in which this is true. There are some tetragonopterine characids, for example *Gymnocorymbus ternetzi* Boulenger and *Hyphessobrycon bifasciatus* Durbin (many populations but not all), that lack predorsal scales. The most parsimonious consideration of the character distributions among these taxa indicates that this is a homoplasy.

The exact extent to which the predorsal scales are absent in *Iotabrycon* is uncertain. All available specimens lack most of their body scales. The scale pockets remain and for the most part can be traced. Both females and males appear to lack scale pockets in the predorsal region dorsal to the narrow pigment stripe along the dorsal border of the abdominal cavity. Scales occur in the epaxial region ventral to the dorsal-fin base and posteriorly to the caudal-fin base, as illustrated by Roberts (1973:491, fig. 1).

25. The maxilla is toothless in both sexes (Figure 59).

Most characids have a toothed maxilla with one to many teeth in a single row along its ventral border. In most glandulocaudines and many tetragonopterines there are one to three teeth anteriorly. Within the Xenurobryconini, *Argopleura* has one to at least three teeth in the maxilla (Figure 66). Other xenurobryconins (Figures 60–65), have the maxillary border from about half toothed to nearly fully toothed (see also apomorphies 46, 60, and 66). The absence of maxillary teeth in some tetragonopterine characids and in *Iotabrycon* represents a homoplasy according to the most parsimonious character distribution.

26. The dorsolateral lamellar process of the anguloarticular bone is absent in both sexes (Figure 59).

In *Argopleura* (Figure 66), *Scopaeocharax* (Figures 60, 61), and *Xenurobrycon* (Figures 63–65) a dorsolateral lamellar process lies external to the dentary bone. The same is true of other glandulocaudines and most other characids.

The anguloarticular process is absent also in the species of *Tyttocharax* (apomorphy 71, Figure 62). The most parsimonious cladogram presented below indicates that this absence is homoplasious.

Subgroup B: *Xenurobrycon*, *Scopaeocharax*, and *Tyttocharax*

Böhlke (1958b:318), Géry (1965:58, 1965b:196), and Mahnert and Géry (1984:512–513) discussed the relationships of the xenurobryconin glandulocaudines as then defined. Although Böhlke used similarities to unite groups of species in his key, his primary emphasis was on differences separating the terminal taxa. Böhlke (1958b:318) stated, "Table 1 lists some [ten categories] of the obvious differences between the xenurobryconin species." But the table, if examined for similarities, list six character transformation series used in the present study as synapomorphies at various levels in the xenurobryconin phylogeny.

Géry (1963:58) looked for similarities useful for relating certain xenurobryconin species and found the posterior position of the anal-fin ray hooks common to the species here referred to *Tyttocharax.* The key constructed by Géry (1965b:196) reflects the utilization of this character.

No claim was made by Böhlke (1958b:318) or Géry (1963:11, 1965b:196, 1977:362) to have studied the relationships of the species then assigned to the Xenurobryconini and Géry (1963:11) made the point that these fishes "are still little known."

Mahnert and Géry (1984:510–512) list five characters common to *Xenurobrycon macropus* and *Tyttocharax madeirae* and suggested that these characters indicate the monophyly of their Xenurobryconini. They also noted the limitation of their study based on their lack of detailed examination of what is here called *Scopaeocharax rhinodus.* While we concur with the use of some of these features, others we find problematical or appropriate to different taxonomic levels. A survey of these features follows.

Their first character is a complex of all the characters they found in the male caudal skeleton. According to their text, these can be separated into about six characters. The first, the presence of a caudal gland covered by a strongly modified and striated scale, is treated here at several taxonomic levels (see our comments on the caudal gland at the "glandulocaudine" level in the Introduction, p. 1, and for the structures of the scale see apomorphies 3, 6, 32, 33, and 57). We find only those aspects of the pouch scales treated here in apomorphies 32 and 33 relevant as subgroup B synapomorphies. Mahnert and Géry (1984:510) found the base of ray 8 of the lower caudal-fin lobe (= our ray 11) enlarged and modified. This equals our apomorphy 28 and is a synapomorphy for subgroup B. (See also our use of this feature in apomorphy 48.) They noted the modified distal end of this fin-ray in *Tyttocharax madeirae* (here used as a synapomorphy for Subgroup C, apomorphy 55). Mahnert and Géry noted one to three reduced rays ventral to the eleventh fin ray, but we find that not all members of subgroup B have this feature and we are able to use a form of it only as a synapomorphy (47) for the species of *Xenurobrycon.* They also used the fusion of hypural one to the parhypural as equivalent to a subgroup B character, but we find that it applies to our more inclusive Xenurobryconini, apomorphy 1. Finally, they noted that hypural 2 is slightly modified. While some shortening of hypural 2 and reduction in its cartilaginous tip may indeed be a synapomorphy of subgroup B, we found the distal shape of the hypural to be quite variable. Thus we do not use this as a character at any level.

Mahnert and Géry (1984:510) noted the dorsally truncated supracleithrum in *Xenurobrycon macropus* and *Tyttocharax madeirae* and indicated it as a possible character for their Xenurobryconini. We find that this character is limited to these two genera. The supracleithrum is much longer in *Scopaeocharax, Iotabrycon,* and *Argopleura* (compare Figures 51–56). On p. 66 we treat this character and find the similarity between *Xenurobrycon* and *Tyttocharax* to be superficial and, even if considered morphologically identical, to be a homoplasy.

Mahnert and Géry (1984:510) found the epioccipital bridge absent in *Xenurobrycon macropus* and *Tyttocharax madeirae* but present in *Scopaeocharax atopodus.* We agree with their observations and find the bridge absent in all species of *Xenurobrycon* (Figure 55) and *Tyttocharax* (Figure 54) examined but present in *Scopaeocharax* (Figures 52, 53). It is equally parsimonious to assume either independent loss of the structure in *Xenurobrycon* and *Tyttocharax,* or loss of the bridge as a synapomorphy of subgroup B xenurobryconins with a reversal in *Scopaeocharax.* Since this feature is ambiguous, we do not use it as a synapomorphy for subgroup B.

A reduced number of branched dorsal-fin rays (6 or 7) was also suggested by Mahnert and Géry (1984:512) as a possible character of their Xenurobryconini. Most American characids have 9 branched dorsal-fin rays, Weitzman and Géry (1981:899), and this is the number found in *Argopleura.* Roberts (1973:492) reported 6 to, usually, 7 branched rays in the dorsal fin of *Iotabrycon praecox.* Böhlke (1958b:322, 324) reported the usual branched dorsal-fin ray count as 7 (one specimen of *S. rhinodus* had 8 rays). We have not used this reductive character as a synapomorphy (see discussion of labile characters in the methods section), but if it were used it would apply to subgroup A xenurobryconins, not subgroup B as indicated by Mahnert and Géry.

Finally, Mahnert and Géry (1984:512) stated that the pelvic fins of males show a clear tendency for elongation. This is noticeably true for species of *Xenurobrycon, Tyttocharax, Scopaeocharax,* and *Iotabrycon.* If this character can be used as described by Mahnert and Géry it would apply to subgroup A. However, many species of characids appear to have slightly to somewhat longer pelvic fin rays in the males than in the females. This is also true for *Argopleura.* We have not applied the character at the level of the Xenurobryconini or for most xenurobryconin subgroups because the character differs subtly among most of these taxa and we lack good outgroup information. However, in *Xenurobrycon,* where the male pelvic fins are quite elongate, we have used the character. The length of the pelvic fin in males of species of *Tyttocharax* varies, with the greatest elongation in *T. madeirae.* (See also comments under apomorphy 53). We have postponed the use of this character for all taxonomic levels except *Xenurobrycon* pending description and redescription of the species of *Scopaeocharax* and *Tyttocharax.*

The following 20 synapomorphies corroborate a hypothesis that the genera of subgroup B are more closely related to one another than any are to *Iotabrycon,* to any other glandulocaudines, or to any other characids.

27. Sexually mature males have the proximal portions of principal caudal-fin rays 10 and 11 arched dorsally, with ray 11 more curved than ray 10 (Figures 11–14). As a result of the greater arch in ray 11, the elongate space between rays 10 and 11, present in males of *Argopleura* and *Iotabrycon* (Figures 8–10), is absent, although rays 10 and 11 may remain widely separated proximally.

Other glandulocaudines and characids show little or no dorsal curvature in rays 10 and 11 (Figures 15–21).

Rays 10 through 12 or 13 show slight dorsal curvature in species of *Mimagoniates* (Figure 19), as does ray 12 in *Landonia latidens* (Figure 18). The curvature is correlated with differently modified fin rays in *Mimagoniates* and a peculiar tissue structure (gland?) in *Landonia* males. We do not consider the similarities homologous. In any case, based on the most parsimonious cladogram, such curvature appears to have evolved independently in these fishes.

28. In sexually mature males the base of principal caudal-fin ray 11, the dorsal ray of the ventral caudal-fin lobe, is hypertrophied into a large unciform dorsally curved process, the proximal tip of which lies lateral to hypural 3 (Figures 11–14).

No such hypertrophy is present in any other glandulocaudines or characids (Figures 8–10, 15–21).

29. In sexually mature males the distal halves of principal caudal-fin rays 7–10 (the ventral rays of the dorsal caudal-fin lobe) curve strongly ventrally. Ray 10 is more strongly curved than ray 7 so that the distal tips of approximately rays 8–10 overlap part of the ventral caudal-fin lobe (Figures 3–7, 67).

Note that these arched fin rays (Figures 11–14, 46, 47) have been drawn out of their natural position so that principal rays 7–12 may be seen in the illustrations. These rays actually extend ventrally almost at right angles past principal ray 13 to reach about principal ray 18.

Iotabrycon praecox (Figures 2, 10, 68) and species of *Argopleura* (Figures 1, 8, 9, 33, 48, 69, 70), display no strongly arched rays, and no other glandulocaudines or characids are known to have principal rays 7–10 in the shape described above, although there may be slight distal ray overlap as in *Argopleura chocoensis* (Figure 69).

The two species of *Brittanichthys* as described by Géry (1965a, figs. 1, 2, 5, 7) show caudal-fin rays, which arch ventrally at their distal ends. In *B. axelrodi* and *B. myersi* only the twelfth ray is so modified and in a very different way than in any xenurobryconin. We conclude on the basis of their dissimilarity that these structures in *Brittanichthys* and in subgroup B xenurobryconins are not homologous and have evolved independently. Both Géry (1965a:14) and Roberts (1973:489) suggested that *Brittanichthys* might be a glandulocaudine. Géry (1977:591) appears to have abandoned that hypothesis, placing it

FIGURE 67.—*Xenurobrycon macropus*, caudal peduncle and fin (lateral view, left side), male, SL 15.4 mm, USNM 219381, Paraguay, Paraguari, Lago Ypacarai.

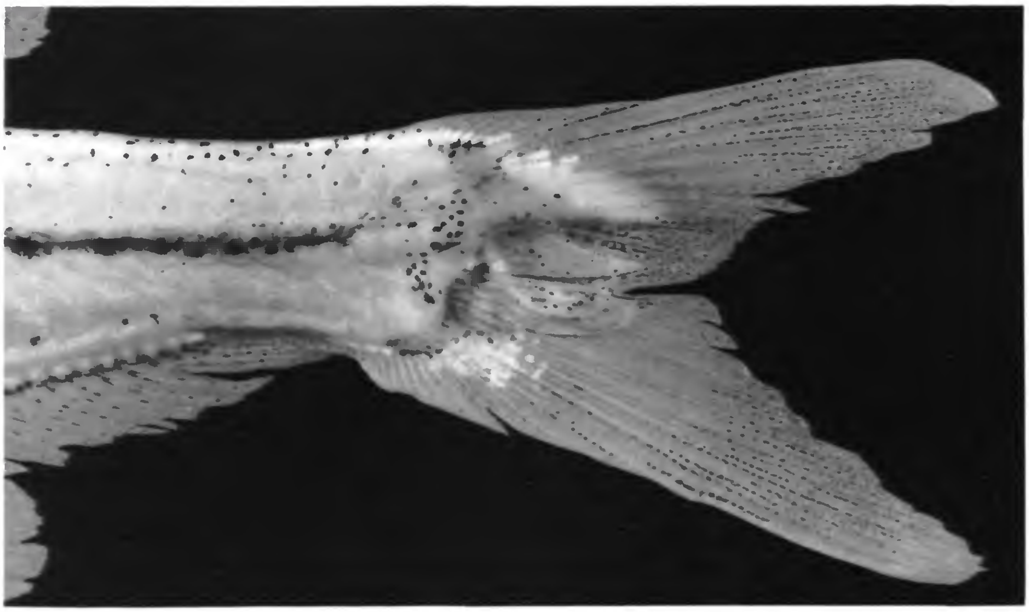


FIGURE 68.—*Iotabrycon praecox*, caudal peduncle and fin (lateral view, left side), male, SL 17.2 mm, USNM 212065, Ecuador, Los Rios, Río Nuevo, tributary of Río Vinces.

FIGURE 69.—*Argopleura* sp., caudal peduncle and fin (lateral view, left side), male, SL 46.3 mm, USNM 220369, Colombia, Cundinamarca, Rio Calandaima, tributary of Rio Bogota.

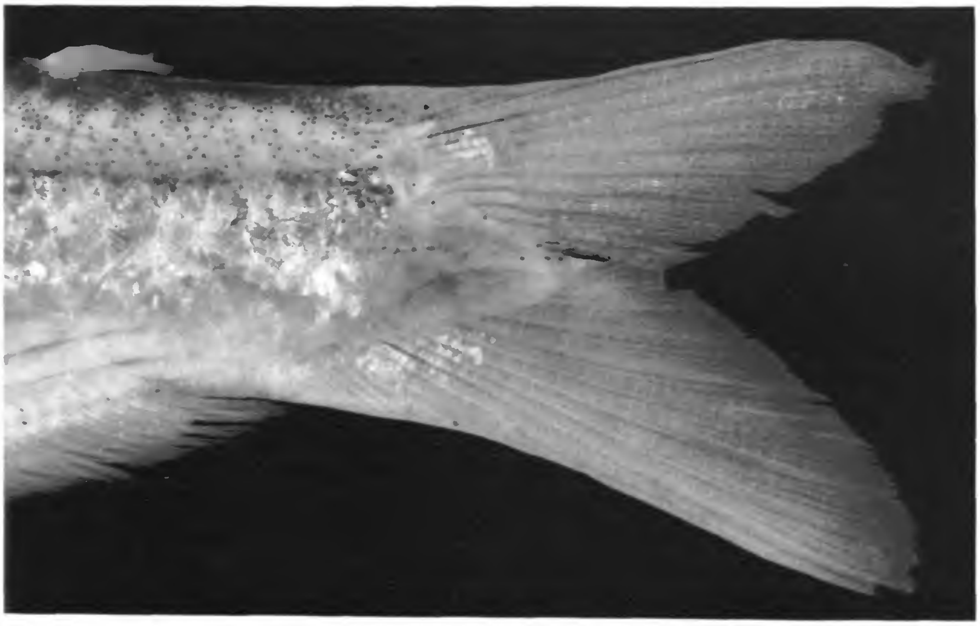


FIGURE 70.—*Argopleura chocoensis*, caudal peduncle and fin (lateral view, left side), male, SL 46.4 mm, paratype, CAS 39030, Colombia, Choco, Rio San Juan, Istmina.

among his "*Aphyodite*-Group" based on characters of tooth morphology. No further reason for this placement is given. Whatever the relationships of *Brittanichthys*, they do not seem to be with the xenurobryconin glandulocaudines. *Brittanichthys* shares none of the synapomorphies listed above for any xenurobryconin.

30. In sexually mature males principal caudal-fin rays 11 through about 14 are very narrow distally and may be shortened (Figures 11–14).

This kind of narrowing is not present in males or females of other characids or glandulocaudines (Figures 8–10, 15–21).

31. In sexually mature males principal caudal-fin rays 1–8 and 16–19 and the largest ventral procurrent ray are expanded in a sagittal plane, with the expansion most marked near the dorsal and especially the ventral margins of the fin (Figures 11–14).

Such expansion is not present in most other glandulocaudines nor in most other characids (Figures 8–10, 15–21). Expansion in a sagittal plane of the rays near the dorsal and ventral margins of the caudal fin is present to a lesser degree in the males of *Glandulocauda* and *Mimagoniates* (Figure 19). Vari (1982:5, fig. 5) recorded an expanded principal caudal-fin ray 19 in the males of some species of *Curimatopsis* Steindachner (1876:81). The most parsimonious hypothesis suggests that such expansions in the two glandulocaudine genera and in *Curimatopsis* are independent of the expansion in subgroup B xenurobryconins.

32. In sexually mature males the hypertrophied posterior field of the pouch scale is horizontally less elongate than in the other xenurobryconins. The greatest vertical depth of the pouch scale varies from about 70 percent to about 115 percent of its greatest horizontal length, depending upon the species examined (Figures 26–31).

In mature *Iotabrycon* and *Argopleura* (Figures 10, 22) the greatest vertical depth of the pouch scale varies from about 52 to 65 percent of its greatest horizontal length. No other glandulocaudines or characids have a terminal lateral line scale modified into a pouch scale, so that there is no single caudal scale to which that of the xenurobryconins could be compared. Caudal scale shape in these outgroups varies from rounded to elongate, depending on the species and position of the scales on the caudal fin. Thus, since a polarity assessment of scale shape is not correctly possible, it is simplest to assume that the shape present in *Argopleura* and *Iotabrycon* is primitive for the Xenurobryconini.

The horizontal length of the pouch scale of *Xenurobrycon heterodon* (Figure 30) is distinctly greater (depth about 72 percent of horizontal length) than that of *X. pteropus* (82 percent) or *X. macropus* (93 percent), *Scopaeocharax* (95 percent), or *Tyttocharax* (115 percent) (Figures 26–29). The elongate shape of the scale of *X. heterodon* is apparently not primitive but a secondary elongation of the posterior field with a concomitant increase in the number of ventral border radii to between 90 and 100. In other *Xenurobrycon* species, *Scopaeocharax*, and *Tyttocharax*, the ventral radii number about 40 to 70, and neither *Argopleura* nor *Iotabrycon* are known to have more than about 40. (See also apomorphy 3.)

33. The pouch scales of sexually mature males have an anteroventrally located process (Figures 26–30).

Such a process is absent in the pouch scales of *Argopleura* and *Iotabrycon* (Figures 10, 22), and in other characids the terminal lateral-line scale lacks such a process. Some specimens of *Argopleura* have a small process in this region, but this process is not consistently present and appears to form part of an irregular, variable border with the accessory pouch scale. We believe it not homologous to the process of subgroup B xenurobryconins. The articulation between the pouch scale and accessory pouch scale in subgroup B xenurobryconins is simple and without the squamosal joint present in *Argopleura*.

In *Iotabrycon praecox* (Figures 10, 23, 32), a short process occurs ventrally and is directed posteriorly. In a developing male 14.7 mm SL this process appears to be part of the posterior border of the scale (compare Figures 10 and 32).

In *Scopaeocharax* and *Tyttocharax* the anteroventral process is quite evident (Figures 26, 27; apomorphy 60). It is also obvious in adult male

Xenurobrycon pteropus (Figure 29). It is less visible in adult male *Xenurobrycon heterodon* (Figure 30) and only a slight process is seen in adult male *Xenurobrycon macropus* (Figure 28). In a late-maturing male of *Xenurobrycon macropus* (Figure 31), the process is even less developed.

The anteroventral process occupies approximately the topographic position of the accessory pouch scale in *Argopleura* (Figure 22) and might represent that scale fused to the large pouch scale. Developmental evidence however, although slight, indicates that the pouch scale develops from a single scale (Figure 31) and that the anteroventral border of the scale develops into the anteroventral process in mature males. There is no evidence of fusion of the accessory pouch scale to the pouch scale in subgroup B xenurobryconins. All projections and processes on the pouch scale appear to be derived by differential growth of parts of the scale rather than by fusion with other bony elements.

34. In sexually mature males the interradialis muscle fibers that insert on principal caudal-fin rays 7-10 cross over adjacent rays, extending much further distally than any other interradialis fibers of the dorsal caudal-fin lobe (Figures 46, 47).

In other characids and glandulocaudines no dorsal-lobe interradialis fibers extend abruptly further than those to adjacent rays (Figures 48, 49). Some dorsal-lobe interradialis fibers are also extensive distally in *Iotabrycon* males (Figure 45); the increased posterior extent of some dorsal-lobe fibers in males may in fact be a synapomorphy for *Iotabrycon, Scopaeocharax, Tyttocharax,* and *Xenurobrycon*. We have not recorded this as a synapomorphy above for subgroup A because we see little actual similarity. In *Iotabrycon* the fibers consist solely of those between adjacent rays, while in *Xenurobrycon, Scopaeocharax,* and *Tyttocharax* the fibers are primarily those that pass over adjacent rays. In addition, in *Iotabrycon* the fibers are extensive distally on rays 5–8, while in *Xenurobrycon, Scopaeocharax,* and *Tyttocharax* it is the fibers inserting on rays 7–10 that are distally extensive. Thus, the only morphology actually present in all four genera, is some distal expansion between ray fibers on rays 7–8, relatively weak evidence of synapomorphy. In any case, the extensiveness of the fibers that pass over adjacent rays with a distal attachment on rays 9 and 10, and the thickness of the muscle distally, are all unique to *Scopaeocharax, Tyttocharax,* and *Xenurobrycon*.

35. In sexually mature males the interradialis muscle fibers that attach to the lateral face of the unciform basal process of principal caudal-fin ray 11 (Figures 46, 47, muscle labeled interradialis-a) form a hypertrophied bundle proximally.

In other glandulocaudines and characids the interradialis fibers originating from principal caudal-fin ray 11 form part of the flat sheet of the ventral caudal-fin lobe interradialis muscles (Figures 45, 48, 49).

36. In sexually mature males a separate bundle of interradialis fibers (labeled as interradialis-b in Figures 46, 47) originates along the lateral face and posterior margin of the unciform process and the dorsal margin of the enlarged base of caudal-fin ray 11 (Figures 11–14). This bundle fans dorsally, posteriorly, and ventrally and inserts near the corresponding borders of the pouch scale.

No separate interradialis bundle of this nature is present in any other glandulocaudines or characids (Figures 44, 45, 48, 49) known to us. Possible functions for the above modified interradialis muscles are suggested in the discussion below on the putative pheromone pumping mechanisms.

37. In sexually mature males all interradialis muscle fibers of the ventral caudal-fin lobe are restricted in extent distally, inserting just beyond the bases of the rays (not visible in Figures 46, 47).

In most glandulocaudines the interradialis muscle of the ventral caudal-fin lobe in sexually mature males (Figures 44, 45, 48) is less extensive than that of the dorsal lobe, but in none are the ventral-lobe fibers so restricted as in *Scopaeocharax, Tyttocharax,* and *Xenurobrycon*. In most characids (Figure 47) the ventral interradialis muscle fibers are as extensive as those of the dorsal lobe.

38. There are 18 or fewer branched anal-fin rays present in both sexes.

The anal-fin ray count varies widely in tetragonopterine characids but a count of 18 or lower is relatively uncommon. Other xenurobryconins and glandulocaudines have 20 or more branched anal-fin rays (except *Glandulocauda melanopleura*, which has 16–18). According to the most parsimonious hypothesis, the relatively low count in xenurobryconin subgroup B evolved independently of other low counts within the Characidae.

39. In sexually mature males and females the cartilaginous portion of the posterior process of the pelvic bone is absent (Figures 36*a,b*, 37*a*).

In other glandulocaudines and characids, except for the gasteropelecines (Weitzman, 1954:260, fig. 18), the pelvic bone has a posterior projection formed of bone proximally and cartilage distally (Figures 35*a,b*, 37*b*). The most parsimonious hypothesis indicates that the absence of the cartilaginous process in gasteropelecines and subgroup B xenurobryconins is a homoplasy.

40. In sexually mature males the pelvic bone is narrow relative to its length, with the distance between the tips of the lateral and posterior processes approximately 33 percent or less of the distance between the tips of the lateral and anterior processes (Figures 36*a,b*, 37*a*).

In other glandulocaudines and characids, the distance between the tips of the lateral and posterior processes is distinctly more than 33 percent of the distance between the tips of the lateral and anterior processes (Figures 35*a,b*, 37*b*).

41. In sexually mature males the anterior tip of the pelvic bone is located anterior to the first pleural rib (rib of the fifth vertebra). The joint between the pelvic bone and the pelvic-fin rays of males occurs at or anterior to the area near the distal tip of the third pleural rib (rib of the seventh vertebra).

In almost all other glandulocaudines and in all characids examined, the anterior tip of the pelvic bone in males and females lies near the distal tip of the second or third pleural rib and the pelvic-fin joint is at a position near the distal tip of the fourth, fifth, or sixth pleural rib.

Species in two other glandulocaudine genera have the pelvic bone and fin anterior in position, but in both sexes. In *Pterobrycon myrnae* (and at least in the male of *Pterobrycon landoni*), the anterior part of the pelvic bone is elongate and its anterior tip is at a position nearer to the cleithrum than to the distal tip of the first pleural rib. The pelvic-fin joint is at a position near the distal tip of the third pleural rib or just posterior to this location. It is usually just slightly posterior in females. In *Corynopoma riisei* both males and females have the anterior part of the pelvic bone elongate and the tip of the pelvic bone is near the distal tip of the first pleural rib. The position of the pelvic-fin joint is like that in *Pterobrycon* males. Although the pelvic girdle positions of *Corynopoma* and *Pterobrycon* on the one hand and of subgroup B xenurobryconins on the other are somewhat similar, they are not exactly the same. Furthermore, based on male caudal-fin morphology, both *Pterobrycon* and *Corynopoma* appear related to the glandulocaudine genus *Gephyrocharax* rather than to any xenurobryconins. Thus the anterior position of the pelvic girdle and fin in *Pterobrycon* and *Corynopoma* appears to have evolved independently of that feature in males of subgroup B xenurobryconins. (See also apomorphies 12, 42, 53, and 62.)

42. In sexually mature females the anterior tip of the pelvic bone is located at a position well anterior to the second pleural rib (rib of the sixth vertebra) and may reach as far anterior as the first pleural rib (rib of the fifth vertebra).

In almost all other glandulocaudines and in other characids the anterior tip of the pelvic bone is located ventral to an area between the second and third pleural ribs. In females of *Corynopoma riisei* the pelvic bone tip lies in an area ventral to the first pleural rib, and in females of *Pterobrycon myrnae* it lies near the postcleithrum. As in the case of the males of these species, the most parsimonious hypothesis indicates the anterior position of the pelvic bone is independently derived in subgroup B xenurobryconins on the one hand and in *Corynopoma* and *Pterobrycon* on the other. (See also apomorphies 12, 41, 53, and 62.)

43. In sexually mature males the medial two pelvic-fin rays of each fin diverge distally from each other much less than other pelvic-fin rays.

In some cases where rays diverge there is a considerable amount of membrane between the rays along their middle length, the amount of membrane diminishing at both the proximal and distal ends (Figure 71). In other cases the rays are held closely parallel by connective tissue and skin (Figures 72, 73). (See also apomorphy 54.)

In other glandulocaudines and characids, including *Argopleura* and *Iotabrycon* (Figure 74), these rays diverge almost as much as the other pelvic-fin rays. In Figures 71–74, the fin rays are drawn only partially spread so that the full variation in extent of interradial membrane is not evident.

44. In adults of both sexes the premaxillary teeth are arranged in two or more diagonal series (Figures 60–65). The median series may comprise only two teeth.

Other glandulocaudines have the premaxillary teeth with only one diagonal row (Figure 59) or in two straight rows (Figure 66).

45. The anterior few teeth of the maxilla of both sexes project somewhat anterolaterally, each slightly more so than the one posterior to it (Figures 60–65).

Other glandulocaudines have the maxillary teeth directed straight ventrally as in *Argopleura* (Figure 66). In *Iotabrycon* maxillary teeth are absent (apomorphy 25). A few nonglandulocaudine characids have maxillary teeth directed laterally but these appear related to other nonglandulocaudine characids rather than to any xenurobryconins.

It may be that this feature is actually a subgroup A character, since it is as parsimonious to assume loss of the derived maxillary tooth state in *Iotabrycon* as loss of the primitive one. However, lacking evidence of such a transformation in *Iotabrycon,* we provisionally place this character at the subgroup B level.

Note: Many subgroup B xenurobryconins have exserted teeth on the jaws (Figures 60, 62, 64, 65). Several different characid groups also have exserted jaw teeth. These are usually fish-scale eaters. (See Roberts, 1970, for a review.) Examination of the stomachs of subgroup B xenurobryconins did not reveal fish scales. Insect (most often ants in fishes from the Amazon basin) and other invertebrate parts were present. The most parsimonious consideration of jaw teeth in subgroup B xenurobryconins and other characid groups indicates independent origin for such teeth in xenurobryconins and these groups.

46. There are usually five or more maxillary teeth in adults of both sexes (Figures 60–65). Small specimens of *Xenurobrycon macropus* sometimes have only four maxillary teeth.

Most other glandulocaudines and characids have one to four maxillary teeth. *Iotabrycon praecox* has none (apomorphy 25). *Hysteronotus* has five to as many as eleven, and *Acrobrycon* has up to eight maxillary teeth. The characids *Rachoviscus* Myers (1926:1) and *Prionobrama* Fowler (1913:534) may have more than four maxillary teeth (Weitzman and da Cruz, 1981:999–1000). *Paragoniates* Steindachner (1876:117) and *Pseudochalceus* Kner and Steindachner (in Kner, 1863:225) also have many maxillary teeth (Géry, 1977:347). The most parsimonious hypothesis indicates that the high number of maxillary teeth evolved independently in subgroup B and in various other characids including the glandulocaudine genera *Acrobrycon* and *Hysteronotus*.

Genus *Xenurobrycon* Myers and P. de Miranda-Ribeiro, 1945

Xenurobrycon Myers and P. de Miranda-Ribeiro, 1945:2 [type-species *Xenurobrycon macropus* Myers and P. Miranda-Ribeiro 1945:5, by original designation].—Ladiges, 1950:309 [discussed possible relationships with *Microbrycon cochui*].—Fowler, 1951:418 [listed].—Myers and Böhlke, 1956:10 [listed].—Böhlke, 1958b:319 [defined in key].—Géry, 1963:11 [discussion, not formally defined].—Nelson, 1964a:70 [mentions "peculiarly sculptured (pouch) scale"].—Géry, 1965b:196 [included in key to species of Xenurobryconini].—Fowler, 1975b:351 [listed].—Géry, 1977:363 [remarks that *X. macropus* not well known].—Mahnert and Géry, 1984:503, 511–512 [discussion of osteology and relationships of *Xenurobrycon* and *Tyttocharax*].

Xenurobricon Fowler, 1951:x [misspelling for *Xenurobrycon*, listed].

Myers and P. de Miranda-Ribeiro (1945:2) described *Xenurobrycon macropus* as new and on page 6 state,

> This remarkable little fish is not very closely related to any known genus of Characidae . . . its dentition, its numerous and disconcerting secondary sexual differences, and its

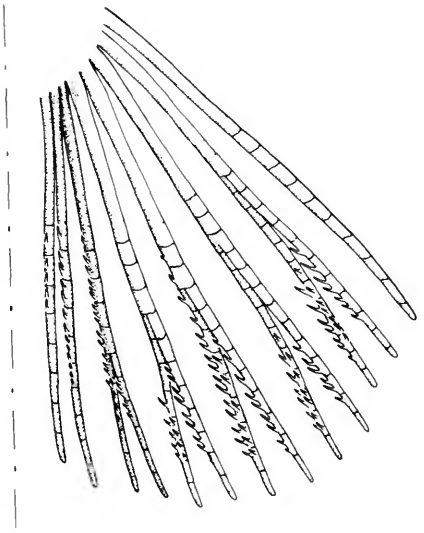


Figure 71.—*Scopaeocharax atopodus*, pelvic-fin rays (ventromedial view, left side), male, SL 21.1 mm, USNM 207517, Peru, Huanuco, Río Huallaga, Tingo Maria. Dashed line indicates midline of body; the fin is slightly spread. In the relaxed fin, the three medial rays distally cross lateral and dorsal to the other rays.

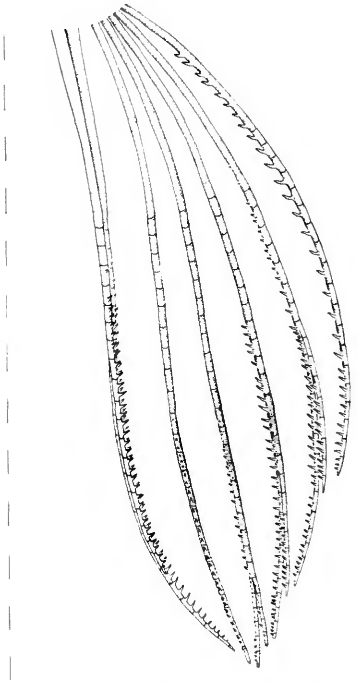


Figure 73.—*Xenurobrycon macropus*, pelvic-fin rays (ventral view, left side), male, SL 15.2 mm, USNM 219381, Paraguay, Paraguari, Lago Ypacarai. Dashed line indicates midline of body; fin rays partially spread.

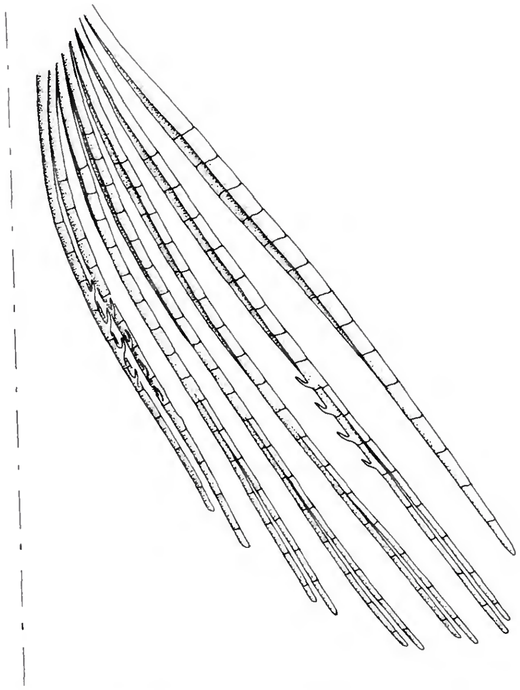


Figure 72.—*Tyttocharax madeirae*, pelvic-fin rays (ventromedial view, left side), male, SL 15.6 mm, USNM 179540, Brazil, Amazonas, Rio Urubú. Dashed line indicates midline of body; fin slightly spread.

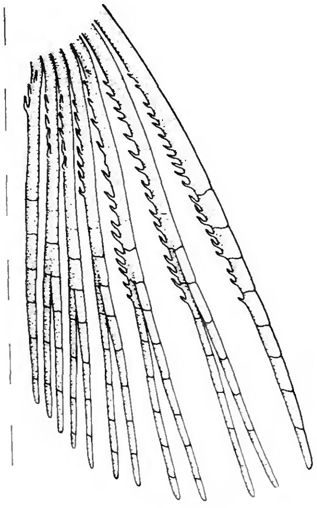


Figure 74.—*Iotabrycon praecox*, pelvic-fin rays (ventromedial view, left side), male, SL 17.7 mm, USNM 217802, Ecuador, Los Rios, Río Palenque. Dashed line indicates midline of body; fin rays slightly spread. If fin was fully spread, the medial two rays would diverge from each other.

> other characteristics make its true systematic position a little difficult to discern . . . suffice it to say that the posteriorly placed dorsal, the fully armed [covered by the third infraorbital bone] cheeks and the elongate form, and above all the caudal gland all indicate very strongly that *Xenurobrycon* belongs with the group that Myers calls the tribe Glandulocaudini . . . . Within the Glandulocaudini, *Xenurobrycon* occupies an isolated position since it differs from all known members of that group in the conical, strictly one-rowed dentition.

Thus Myers and P. de Miranda Ribeiro interpreted the "position" of *Xenurobrycon* strictly within Eigenmann's system of classification and use of "generic" characters. For critical review of this approach see discussion by Weitzman and Fink (1983:339–345). Ladiges (1950:308) and Myers and Böhlke (1956:6) recognized a relationship between *Xenurobrycon* and *Tyttocharax* (see discussion under *Tyttocharax*). Böhlke (1958b:318) was unsure of the nature of the relationship between *Xenurobrycon* and *Tyttocharax* but considered the genera closely related. Géry (1963:13, 1977:363) did not discuss the relationships of *Xenurobrycon*. Mahnert and Géry (1984:512) described parts of the osteology of *Xenurobrycon macropus* and presented a diagram of the relationships of *Xenurobrycon macropus* and the species of *Tyttocharax* (including those here placed in *Scopaeocharax*). They found *Xenurobrycon* to be the sister group of *Tyttocharax* (= our subgroup C).

DIAGNOSIS.—The following seven features are hypothesized to be synapomorphies of *Xenurobrycon* and constitute a diagnosis of the genus.

47. In sexually mature males the ossification of caudal-fin rays 11, 12, and sometimes 13, is interrupted proximally (Figure 11).

In other subgroup B xenurobryconins, rays 11, 12, and 13 may be irregularly ossified (or occasionally unossified) distally (Figures 13, 14). *Argopleura*, *Iotabrycon*, other glandulocaudines, and other characids have no interrupted caudal-fin rays.

48. In sexually mature males the unciform (proximal) process of principal caudal-fin ray 11 is elongate, being about equal in its longest dimension to the length of the posterior border of the fused parhypural plus hypural 1 element (Figure 11).

In other subgroup B xenurobryconins the longest dimension of the unciform process is considerably shorter (Figures 13, 14).

49. In sexually mature males the ventral borders of the ventral unbranched principal caudal-fin ray and the adjacent procurrent fin ray are distinctly concave in the region near the terminal few segments of the anteriorly adjacent ray (Figure 11).

In other sexually mature male xenurobryconins these rays are either straight or shallowly concave (Figures 8, 10, 14). Among other glandulocaudines no real concavity is present, except in *Gephyrocharax* (Figure 17), *Glandulocauda*, and *Mimagoniates* (Figure 19), which have a similar concavity on the largest ventral procurrent ray. On the basis of the most parsimonious hypothesis, the concavities in *Xenurobrycon* are considered to have evolved independently of the similar feature in *Gephyrocharax, Glandulocauda,* and *Mimagoniates*.

50. In sexually mature males the pouch-scale ligament is relatively weak and loosely organized. Its attachment to the pouch scale is split primarily into two areas on the apical region of the posterior field of the scale (Figure 34*c, d,* and *e*).

Other xenurobryconins never have the pouch-scale ligament weak and loosely organized. Its attachment to the pouch scale is always in a single area (although its attachment to the fin rays is in two parts when it attaches to rays 10 and 11 instead of only to ray 11). (See also apomorphies 4, 55, 58, and 59.)

The loose, weak organization of the pouch-scale ligament could be intepreted as primitive within xenurobryconins, based on its morphology. According to the most parsimonious cladogram, however, the character is a reversal.

51. In sexually mature males the pelvic bones are separated posteriorly so that a space three to five times the length of the medial posterior processes, or greater than one-third of the length of the pelvic bone, extends between the posterior processes (Figure 37*a*). As a result, as Böhlke (1958b:319) noted, the "bases of ventral fins of males [are] separated widely and placed rather high on the sides."

Other xenurobryconins, glandulocaudines, and characids examined have the posterior as well as the anterior ends of the pelvic bones adjacent (Figures 35, 36, 37*b*).

52. In sexually mature males the ventral surface of each pelvic bone has a large ventral lamella extending from the lateral process across the pelvic plate anteromedially to the midlength of the medial border of the bone (Figure 37*a*). This process serves as an additional surface of origin for very large arrector dorsalis pelvicus and abductor profundus pelvicus muscles.

We found no other xenurobryconin, glandulocaudine, or characid with this large ventral pelvic lamella (Figures 35, 36, 37*b*).

53. In sexually mature males the anterior end of the pelvic bone lies near the cleithrum and the posterior end lies at a position near the second rib.

Other xenurobryconins, glandulocaudines, and characids known to us have neither the anterior nor the posterior ends of the pelvic bones this far anterior. (See also apomorphies 12, 41, 42, and 62.)

54. Sexually mature males have the following pelvic-fin modifications: the fin is approximately one-third the total length of the fish; the interradial membrane is extremely expansive in the middle region of the fin but narrows considerably distally so that the tips of the rays approach each other closely; when the fin is extended and spread with forceps it forms an inverted boat-shaped canopy (Figure 73).

In other xenurobryconins, glandulocaudines, and characids, the pelvic fin in mature males is no longer than about one-fourth the total length of the fish, the interradial membrane is less expansive, and the distal tips of the rays do not approach each other as closely. (See also apomorphy 43.)

Tyttocharax madeirae and some closely related (undescribed) species have a fairly elongate pelvic fin, which extends posteriorly well past the origin of the anal fin (Figure 6). This pelvic fin also may form something of a canopy when extended and spread. This feature is not present to such a degree in *Tyttocharax cochui* and in some additional undescribed species. It is hypothesized that the large form of the fin evolved independently in *Xenurobrycon* and a subgroup of *Tyttocharax*.

Subgroup C: *Scopaeocharax* and *Tyttocharax*

The following six synapomorphies corroborate the hypothesis that *Scopaeocharax* and *Tyttocharax* are more closely related to one another than to species of other xenurobryconin subgroups or other characids.

55. In sexually mature males principal caudal-fin rays 10 and, especially, 11 are hypertrophied distally at the attachment site of a strong, thick pouch-scale ligament. Fin-ray 11 narrows abruptly or terminates just distal to the thickened portion (Figures 13, 14). The thickened portions of these fin rays have several fin-ray segments fused.

No other xenurobryconins, glandulocaudines, or characids are known to have principal caudal-fin rays 10 and 11 modified in this manner. Principal caudal-fin ray 11 in *Xenurobrycon* sometimes may be a little thickened at the point of attachment of the pouch-scale ligament (Figure 11), but the ray is never much thickened as in Figure 13 and never club-shaped as in Figure 14 (See also apomorphies 4, 50, 58, and 59.)

56. In sexually mature males the distance between the bases of caudal-fin rays 10 and 11 (measured from the ventral border of ray 11, thus excluding the unciform process from the measurement) is approximately equal to or less than the vertical length of the posterior margin of hypural 3 (Figures 13, 14).

In other sexually mature male xenurobryconins the distance between the bases of caudal-fin rays 10 and 11 is greater than the vertical length of the posterior border of hypural 3 (see apomorphy 2). Other characids, however, including nonxenurobryconin glandulocaudines, have a condition similar to that in *Scopaeocharax* and *Tyttocharax*. The lesser distance for this measurement in subgroup C xenurobryconins is a reversal or innovation according to the most parsimonious cladogram and therefore a synapomorphy for *Scopaeocharax* and *Tyttocharax*.

57. The pouch scale of sexually mature males has an anteroventral notch and accompanying anteroventral lobe or process well developed and large (Figures 26, 27).

A notch and lobe are absent in the pouch scales of species of *Argopleura* and *Iotabrycon* (Figures 10, 22; see also apomorphy 33). Species of *Xenurobrycon* have a very shallow notch and a modest anteroventral process, which sometimes is represented as an angular corner of the scale (Figures 28–30).

58. The pouch-scale ligament of sexually mature males is short and thick, of dense regular connective tissue, with a single, large area of attachment to the medial pouch-scale wall distally and to the closely adjacent thickened areas of rays 10 and 11 proximally (Figure 34*a,b*).

Iotabrycon and *Argopleura* have the ligament long, less thick, and attached to the medial posterior border of the pouch scale (Figures 32, 33). In *Xenurobrycon* the pouch-scale ligament is short but relatively weak and its attachment to the pouch scale is divided roughly into two parts (Figure 34*c–e*). (See also apomorphies 4, 50, 55, and 59.)

59. The pouch-scale ligament attachment of sexually mature males is confined to the midregion of the medial wall of the pouch scale (Figure 34*a,b*).

In other xenurobryconin glandulocaudines the pouch-scale ligament attaches to the medial wall of the posterior apex or apical part of the pouch scale (Figures 33, 34*c–e*). In *Iotabrycon* the ligamentous attachment extends narrowly from the apex toward the midregion of the scale (Figure 32), but the attachment is primarily in the apical portion and is not restricted to the midregion of the scale as it is in subgroup C.

60. The maxillae of adult males are nearly fully toothed, each usually bearing about 20–25 teeth along its entire ventral border (Figures 60–62).

No other xenurobryconin group has nearly fully toothed maxillae (Figures 59, 63–66). (See apomorphies 25, 46, and 66 for further outgroup information.)

Genus *Scopaeocharax*, new genus

Tyttocharax.—Böhlke, 1958b:319 [in part, diagnosis in key].—Géry, 1963:11 [in part, discussion of generic placement, mostly after Böhlke, 1958b:315].—Nelson, 1964a:63, 70 [in part, caudal scale structure of *Tyttocharax rhinodus*].—Géry, 1977:362 [in part, discussion of species].—Mahnert and Géry, 1984:511–512 [in part, discussion of relationships].

TYPE-SPECIES.—*Tyttocharax rhinodus* Böhlke (1958b:320). The genus also includes *Tyttocharax atopodus* Böhlke (1958b:323). (See *Tyttocharax* for a history of proposed relationships for the species in this genus.)

DIAGNOSIS.—The following six synapomorphies form a diagnosis for *Scopaeocharax* and corroborate the hypothesis that the two species listed above form a monophyletic group.

61. In sexually mature males, rugosities are present along the dorsal margin of the distal hypertrophied area of principal caudal-fin ray 10 (Figure 13). (This area lies just medial to the posterior process of the pouch scale.)

No other glandulocaudine or characid is known to have such rugosities (Figures 8–12, 14) although very slight rugosities sometimes occur in *Tyttocharax*.

62. In sexually mature females the anterior tip of the pelvic bone lies in the region ventral to the distal ends of the anterior pleural ribs (ribs of vertebra 5).

In female specimens of *Tyttocharax madeirae, T. cochui*, and the three species of *Xenurobrycon* the anterior tip of the pelvic bone lies in the area between or ventral to the first and second pleural ribs. In almost all other glandulocaudines and characids examined it extends to the area ventral to the second or third pleural ribs, or between them. (See also apomorphies 12, 41, 42, and 53.)

In *Corynopoma riisei* females (and males) the anterior end of the pelvic bone lies in the same position as in *Scopaeocharax* females, and in both sexes of *Pterobrycon myrnae* Bussing (1974:138) the anterior tip of the pelvic bone lies anterior to the first large pleural rib. According to the most parsimonious hypothesis of relationships of these taxa, this character appears homoplasious in *Corynopoma* and *Pterobrycon* relative to the condition in *Scopaeocharax*.

63. In sexually mature males the medial two or three pelvic-fin rays curve dorsal to the rest of the rays when the fin is relaxed or folded (the fin is partially spread in Figure 71).

In males, females, and juveniles of other glandulocaudines and characids (and in females and juveniles of *Scopaeocharax*), the medial two or three rays lie in a series medial to the other fin rays when the fin is relaxed or folded.

64. In a lateral view of the orbit the dorsal margin of the parasphenoid and the ventral margin of the pterosphenoid are close or in contact (Figures 52, 53).

In other glandulocaudines (Figures 51, 54, 56) and characids (Figure 57) (see also Weitzman and Fink, 1983, figs. 4–15) a portion of the prootic lies between and separates the parasphenoid and pterosphenoid.

65. The premaxilla is short, its length from the anteromedial to the posterolateral borders approximately equal to its height, including the teeth (Figures 60, 61).

In other glandulocaudines and most other tetragonopterine characids the premaxilla is longer, its length distinctly greater than its height (Figures 59, 62–66). (See also Weitzman and Fink, 1983, figs. 19–22, and Fink and Weitzman, 1974, figs. 7, 9, 13, 16, 20, 21, 23, 25.) Note that these figures show a large amount of variation in the length of the posterior premaxillary process, something we find in many characids. Also, these figures often do not give a full measure of the premaxillary length versus height due to somewhat varying angles of view. However, in all cases, the length of the premaxilla, when measured from the anterior tip of the premaxillary bone to the tip of the posterior premaxillary process, is greater than its height, the distance between the anterior tip of the premaxilla and the posterodorsal tip of the ascending process.

66. A nearly complete row of teeth are present along the ventral border of the maxilla in adult females as well as adult males.

No other xenurobryconin has a nearly complete row in both sexes although the males of *Tyttocharax* have a nearly complete row (see apomorphies 25, 46, 60).

Some glandulocaudines, for example *Acrobrycon*, have a well-toothed maxilla in both sexes, but in view of the many synapomorphies placing *Scopaeocharax* as a xenurobryconin the similarity is most parsimoniously considered a homoplasy. In several characid genera, for example *Prionobrama*, both sexes have a nearly fully toothed maxillary bone (Weitzman and da Cruz, 1981:1000); but again, parsimony would indicate this similarity to be a homoplasy.

Genus *Tyttocharax* Fowler, 1913

Tyttocharax Fowler, 1913:563 [type-species: *Tyttocharax madeirae* Fowler, 1913:564, by original designation]; 1951:418 [listed].—Myers and Böhlke, 1956:8 [diagnosis and discussion of relationships].—Böhlke, 1958b:315 [in part, discussion of relationships, placement of *Microcaelurus* as a junior synonym of *Tyttocharax*].—Géry, 1963:11 [in part, discussion of generic synonymy, mostly after Böhlke (1958b:315), field photographs of live specimens of *Tyttocharax madeirae*]; 1965b:195 [in part, description of a new species]; 1966:211 [in part, species citation]; 1977:362 [in part, brief discussion of species].—Mahnert and Géry, 1984:511–512 [in part, discussion of osteology and relationships].

Microcaelurus A. de Miranda-Ribeiro, 1939:362 [type-species: *Microcaelurus odontocheilus* A. de Miranda-Ribeiro, 1939:362, by monotypy].—Myers and Böhlke, 1956:11 [listed, discussion of type locality of type species, translation of original Portuguese description into English].—Mahnert and Géry, 1984:512 [question taxonomic status].

Microbrycon Ladiges, 1950:305 [not of Eigenmann and Wilson in Eigenmann, Henn, and Wilson, 1914:3, mistaken generic allocation of a new species of *Tyttocharax*, *Microbrycon cochui* Ladiges, 1950:308].

Fowler (1913:563) described *Tyttocharax madeirae* as new and placed it in the Characinae commenting that the genus shows "affinity with certain of the Tetragonopterinae [unspecified] in the large scales, but the conical teeth and external tooth-like processes are more features of the present subfamily [Characinae]."

A. de Miranda-Ribeiro (1939:362) described a new genus and species of characids, *Microcaelurus odontocheilus,* now considered a junior synonym of *Tyttocharax madeirae* (see latter species in Appendices 1 and 2). He noted that the fish had the body form of *Hemibrycon beni* Pearson (1924:42) and the dentition of *Exodon paradoxus* Müller and Troschel (1844:91) but made no substantive comments about relationships.

Ladiges (1950:308) in a supplement to his description of *Tyttocharax cochui* was the first to recognize and publish on similarities between

Tyttocharax and *Xenurobrycon*, noting superficial likenesses in the tail regions. Ladiges did not investigate these similarities in any detail nor propose any formal classification based on his observations. Ladiges (1950:305–306) considered these genera allied to the Glandulocaudinae. Fowler (1951:415, 418) placed *Tyttocharax* with the Glandulocaudinae without comment. He also placed *Tyttocharax* and *Xenurobrycon* next to each other in his list but this is a result of his practice of alphabetizing genera within family and subfamily groups.

Myers and Böhlke (1956:6) formalized their observations about the relationships of *Tyttocharax* and *Microcaelurus* with *Xenurobrycon* by establishing the Xenurobryconini, noting that these three genera are allied to each other. They removed *Xenurobrycon* (and thus its putative relatives) from the Glandulocaudini (= Glandulocaudinae) where it had been placed by Myers and Miranda-Ribeiro (1945:6). Myers and Böhlke (1956:6) remarked that the "strange, irregular arrangement of the teeth of these fishes precludes placement anywhere in Eigenmann's [classification] system, although the male caudal gland indicates a close relationship with the genera grouped by Eigenmann . . . in the Glandulocaudinae. . . ." They further noted that the Xenurobryconini are "tiny characids closely allied to the Glandulocaudini. . . ." They listed several characters, some of which are still useful and are expressed in more detail as part of the apomophies listed here for Subgroup B.

Böhlke (1958b:318), on reconsideration of evidence in the literature, decided that *Microcaelurus* was a junior synonym of *Tyttocharax*. (We have examined the types and confirm Böhlke's decision; see note in Appendix 2 under *Tyttocharax madeirae*). Böhlke (1958b:320, 323) described two new species of *Tyttocharax, rhinodus* and *atopodus,* and remarked that "generic limits are not now apparent in these fishes [all the xenurobryconins]," but recognized *Tyttocharax* and *Xenurobrycon*.

Géry (1963:11–15) briefly reviewed the species of *Tyttocharax*, based on the literature and a new collection of *Tyttocharax madeirae* from near Belém, Pará, Brazil, and a collection from Lago Tefé, Amazonas, Brazil. He also examined photographs and/or specimens of *Tyttocharax cochui.* According to Géry the back and white photographs had been prepared by Otto Schindler for an unpublished paper designating *Tyttocharax cochui* a junior synonym of *Tyttocharax madeirae.* Géry (1963:14–15) accepted the hypotheses of Myers and Böhlke (1956:7) and Schindler (unpublished) that *Tyttocharax cochui* is a junior synonym of *Tyttocharax madeirae.* Géry (1963:59) suggested the possibility that *Microcaelurus odontocheilus* is a junior synonym of *Tyttocharax madeirae,* something we confirm in Appendix 2 (p. 109). Géry (1963:12, 13) published two useful color photographs of *Tyttocharax madeirae* showing life (or near life) colors but did not discuss the relationships of the species or the group except to state that the xenurobryconins are relatives of the glandulocaudines. Géry (1965b:195) described a new species, *Tyttocharax boehlkei,* from near the type locality of *Tyttocharax cochui.* In Appendix 2 (p. 110) we present evidence suggesting that the former may be a junior synonym of the latter. Géry (1965b:196) suggested that *Tyttocharax madeirae* and his *Tyttocharax boehlkei* are more closely related to each other than to *Tyttocharax rhinodus* or *Tyttocharax atopodus,* because of the presence of hooks on the posterior anal-fin rays in males in the former two species and a few other differences between these two groups of species. We use some of these features as synapomorphies relating the species of *Tyttocharax,* and others of these features relating the species of *Scopaeocharax* (see apomorphy 67). Géry (1966, 1977) added no new information on *Tyttocharax* or *Scopaeocharax.* Mahnert and Géry (1984:509) briefly described parts of the osteology of *Tyttocharax madeirae* and considered this species related to *Xenurobrycon macropus.*

DIAGNOSIS.—The following features are hypothesized to be synapomorphies of *Tyttocharax.*

67. In sexually mature males bony hooks are confined to the posterior six to eight anal-fin rays, except for the termi-

nal ray, which is without hooks (Figure 41). These hooks are relatively large and arranged on the fin in a vertically elongate cluster.

Other sexually mature male xenurobryconins may have hooks on some or all of these posterior rays, but in these species the hooks are not confined to that region and they are not arranged in a vertically oriented cluster. Some species of *Argopleura* (apomorphy 7) occasionally have small posterior hooks. *Scopaeocharax* (Figure 40) has small hooks distributed over much of the anal fin. The distribution of hooks in *Xenurobrycon macropus* (Figure 42) is typical of that in many subgroup B xenurobryconins. The anal-fin hooks of *Xenurobrycon pteropus* (Figure 43) are relatively large and occur on eight of the 11 posterior rays of the fin (they are absent on the terminal three). However, they are not arranged in a vertically oriented cluster. *Argopleura* (apomorphy 7) has lost hooks on one to three anal-fin rays in the anterior half of the fin. Either of these arrangements might be interpreted as steps in a transition series leading to the kind of anal-fin hook placement and development found in *Tyttocharax*, but the most parsimonious cladogram indicates an independent derivation for the hook configuration in *Tyttocharax* species, *Xenurobrycon pteropus*, and species of *Argopleura*.

68. In sexually mature males the posterior three to five proximal anal-fin radials are expanded into flattened plates serving as the origin for very robust erectores and depressores anales muscles. These plates abut one another. Furthermore, the bases of four or five posterior fin rays are enlarged for the insertion of the tendinous portions of these muscles (Figure 75).

Mature males of most other xenurobryconins have very slender posterior proximal radials except for the most posterior, which is a little larger than the others. The accompanying musculature is relatively small, like that of other glandulocaudines and characids, and the fin-ray bases are not large (Figure 76).

The species of *Xenurobrycon* have the posterior seven to ten proximal radials somewhat expanded and the posterior one broadly expanded (Figures 77, 78). The most parsimonious cladogram indicates either that the expansion in *Tyttocharax* and *Xenurobrycon* is separately derived or that some expansion is a synapomorphy of subgroup B with a reversal in *Scopaeocharax*. Since the evidence may be interpreted either way, we have not included either of these hypotheses in the characters section. In any case, the extreme expansion and associated features are unique to *Tyttocharax*.

69. Mature males and females have four to seven diagonal rows of conical teeth in each premaxilla, each premaxilla having about 25 to 40 teeth (Figure 62). There is some variation in tooth-row number and total tooth number depending on the species and the size of the specimen. Males and females of equal lengths in a given species have nearly the same number of teeth and tooth rows. Large females (as well as large males) will have higher counts than small males or females.

Other xenurobryconins have one to three rows of premaxillary teeth, with a total of less than 20 teeth and often fewer than 8, depending on the species examined (Figures 59–61, 63–66). Other glandulocaudines have two premaxillary tooth rows and fewer than 10 teeth on each premaxilla. Most characids have fewer than 10 premaxillary teeth in one, two, sometimes three and rarely four, rows. Those characids with a large number of tooth rows and teeth appear unrelated to *Tyttocharax* according to the most parsimonious hypothesis of relationship.

70. Mature males and females have four to eight rows of dentary teeth, all but the innermost diagonal, with a total of 50 to 80 or more teeth on each mandible. Many of the teeth project anteriorly or laterally (Figure 62). There is some variation in tooth-row number and total tooth number depending on the species examined and the size of the specimen.

Other xenurobryconins have one to rarely two rows of dentary teeth with a total of less than 20 teeth and often fewer than 10, depending on the species examined (Figures 59–61, 63–66). Other glandulocaudines and most other characids have one row of dentary teeth. Those characids with two rows of teeth have the second row internal to the main dentary row, rather than external, and usually the inner row is represented by a

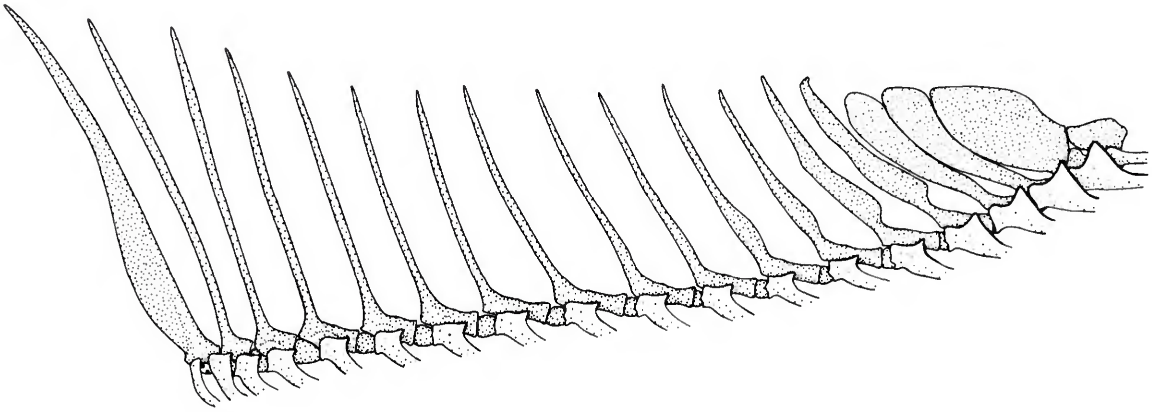


Figure 75.—*Tyttocharax madeirae*, anal-fin pterygiophores and bases of anal-fin rays (lateral view, left side), male, SL 15.4 mm, USNM 179540, Brazil, Amazonas, Rio Urubú. Flattened and expanded posterior proximal radials serve as surfaces of origin for musculature inserting on rays bearing large hooks.

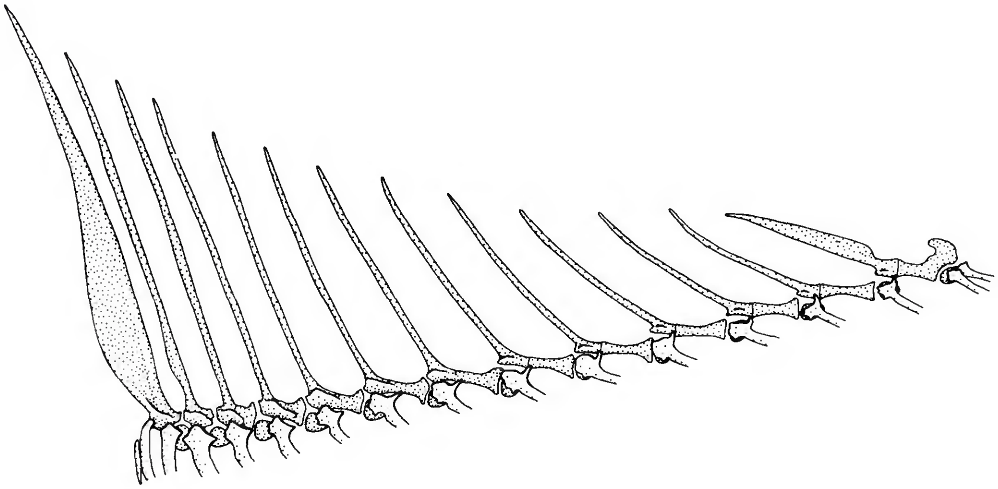


Figure 76.—*Scopaeocharax atopodus*, anal-fin pterygiophores and bases of anal-fin rays (lateral view, left side), male, SL 21.1 mm, USNM 207517, Peru, Huanuco, Río Huallaga, Tingo Maria.

single inner tooth on each dentary near the symphysis.

71. The dorsolateral lamellar processes of the anguloarticular bone is absent (Figure 62).

Most other characids, other glandulocaudines, *Scopaeocharax* (Figures 60, 61), *Xenurobrycon* (Figures 63–65), and *Argopleura* (Figure 66) have a dorsolateral lamellar process external to the dentary bone. The process is also absent in *Iotabrycon* (Figure 59). This absence is most parsimoniously interpreted as homoplasious (see apomorphy 26).

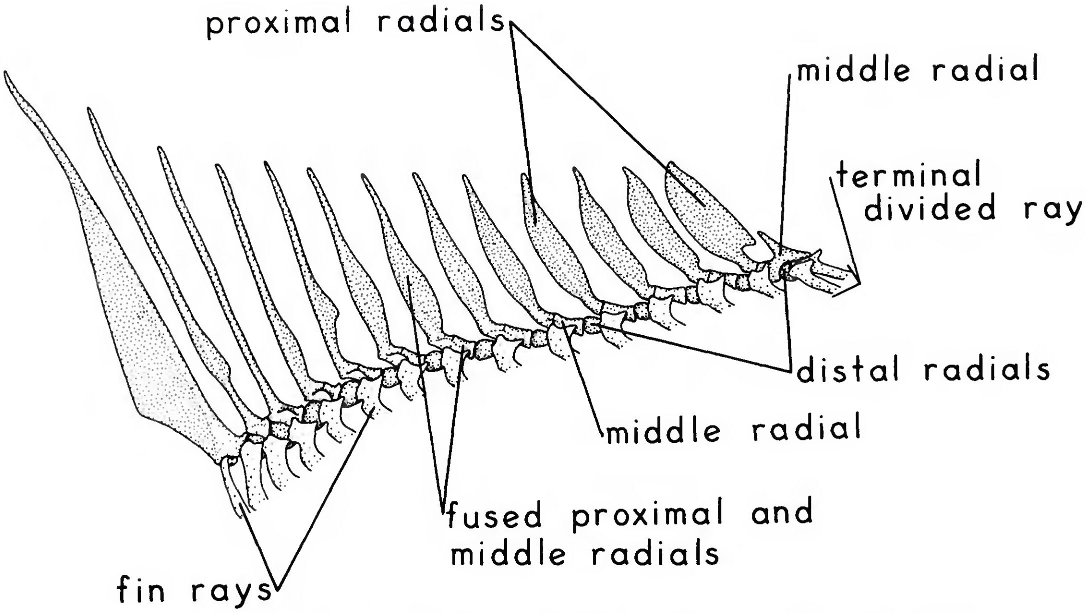


FIGURE 77.—*Xenurobrycon macropus*, anal-fin pterygiophores and bases of anal-fin rays (lateral view, left side), male, SL 14.4 mm, USNM 219381, Paraguay, Paraguari, Lago Ypacarai.

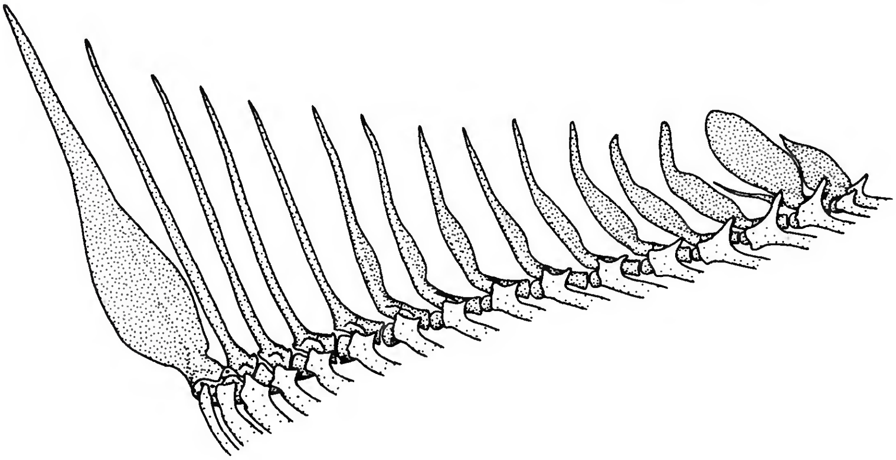


FIGURE 78.—*Xenurobrycon pteropus*, anal-fin pterygiophores and bases of anal-fin rays (lateral view, left side), male, SL 13.8 mm, paratype, USNM 232921, Brazil, Amazonas, Fonte Boa.

Discussion

The xenurobryconin features we found to be synapomorphies are primarily of two kinds, reductive or loss characters apparently associated with small adult size, and innovative characters not found in other fishes. The latter characters usually form parts of the secondary sexual features of the males. Some of both innovative and reductive characters are associated with small size and may be associated with increased resistance of water to flow in tiny tubes (pp. 32, 97). For the most part we found congruence among the distributions of the two kinds of characters in the taxa studied. Each of the nine groups formulated from the distribution of the 71 apomorphies listed above is discussed briefly below and problems raised by conflicting characters are outlined.

The monophyly of the Xenurobryconini is documented by five (1–5) synapomorphous sexually dimorphic characters confined to the males (except fusion of the parhypural and hypural 1, which occurs also in females of *Iotabrycon*). Four of these (apomorphies 1–4) are associated with, or are part of, the caudal-fin structure and the fifth is part of the pelvic fin. Most of these features, such as the posterior terminal lateral-line scale being a large pouch scale and the presence of a pouch-scale ligament, undergo further divergent elaboration in subgroups of the Xenurobryconini. We found only one inconsistent character at this taxonomic level. The wide separation between the bases of caudal-fin rays 10 and 11 in mature males (apomorphy 2) is not as pronounced in subgroup C (apomorphy 56), suggesting that *Argopleura, Iotabrycon,* and *Xenurobrycon* form a group. Such a grouping is not supported by any other derived feature. The previous suggestion (p. 13) that xenurobryconin characids are related to other characids with conical teeth would apply only to subgroup A and is considered under that subgroup (p. 63).

Argopleura is the sister group to the remaining xenurobryconins and is the least derived morphologically for the characters considered here, retaining many tetragonopterine features, as well as having the basic xenurobryconin synapomorphies. The species of *Argopleura* are hypothesized to have shared a unique common ancestor based on two synapomorphies (6, 7), both associated with male secondary sexual characters. One is a caudal pump specialization; the other is a special pattern of anal-fin hooks. We found no characters conflicting with these synapomorphies.

It should be noted further that, with the exception of the erroneous assignment of a caudal fulcrum or spur to *Argopleura* by Eigenmann (1913:10) and Géry (1966:227, 1977:358), none of the authors cited in this paper have tried to relate *Argopleura* to *Bryconamericus, Planaltina,* or *Gephyrocharax* on the basis of shared specialized characters, although they have suggested various relationships among these genera. *Bryconamericus* or some part of it might be the sister group of the Xenurobryconini, but this problem was not investigated extensively here because it is tied to the complex problem of the monophyly of the Glandulocaudinae.

Subgroup A (*Iotabrycon, Xenurobrycon, Scopaeocharax,* and *Tyttocharax*) has both innovative secondary sexual characters and reductive modifications. As mentioned below (p. 97), both kinds of these derived features may be related to small size (apomorphies 8, 18).

There are some secondary sexual caudal muscle reductions in males (apomorphies 9, 10), which may have more to do with the varied caudal muscular innovations of subgroup A males than with loss associated with small body size (p. 30). We cannot be certain whether these shared muscle reductions are coincidental, since they are the only shared specialized muscle features of two different pumping mechanisms, or whether they are indicative of a common morphology once shared by these two now divergent lines (*Iotabrycon* and subgroup B). We incline toward the latter hypothesis because these characters are congruent with other characters indicating the same phylogenetic hypothesis. Furthermore, innovative features, such as the anterior position of the pelvic bones (apomorphy 12) and the peculiar arrangement of the jaw teeth (apomorphy 16), corroborate subgroup A.

Subgroup A species also share loss of pores in the lateral line (apomorphy 8) and some laterosensory canal reductions associated with the posterior part of the head (apomorphies 13–15). These reductions are common in small characids (Weitzman and Fink, 1983:343, 391–394). Because all subgroup A species are small, these characters might be relatively poor indicators of relationship and are perhaps subsets of apomorphy 18, small size. However, we found almost no features corroborating hypotheses of relationship contradictory to that accepted here for subgroup A (p. 64) and to us the congruence of morphological features at this level is convincing. Weitzman and Fink (1983:391–394) rejected as synapomorphous certain laterosensory canal system reductions in *Paracheirodon* for lack of precise outgroup hypothesis. In the present case, *Argopleura* forms a precise outgroup to subgroup A xenurobryconins, and therefore we believe it appropriate to use synapomorphies 8 and 13 to 15. A similar case can be made for recognizing synapomorphy 17 (conical jaw teeth), even though some other small characids are known to have conical teeth, for example, the "Aphyoditeina" of Géry (1977).

Nine other possible characters of subgroup A need discussion. One is a short maxilla. In *Iotabrycon* and *Xenurobrycon* the maxilla does not extend posteriorly beyond a vertical line drawn through the anterior border of the eye. However, *Scopaeocharax* and *Tyttocharax,* like *Argopleura* and most other glandulocaudines, have relatively long maxillae. That bone extends well posterior to the anterior border of the eye in *Scopaeocharax,* and to or a little past that point in *Tyttocharax.* While the presence of a short maxilla may be a synapomorphy of subgroup A, with a subsequent reversal in subgroup C, it is equally parsimonious to assume that a short maxilla evolved independently in *Iotabrycon* and *Xenurobrycon.* Therefore we have not used this character.

Another possible character for subgroup A, presence of bony hooks on the pelvic fins of adult males, has an uncertain polarity. Bony hooks are absent on the pelvic fins of adult, sexually mature males in all the species of *Argopleura* examined (unknown for *A. conventa* Eigenmann for which we had no males). Adult males of all other xenurobryconins, most other glandulocaudines, and many other characids have pelvic-fin hooks. However, many characids lack pelvic-fin hooks. Within *Bryconamericus,* for example, *Bryconamericus beta* Eigenmann (USNM 259089) and *Bryconamericus caucanus* Eigenmann (USNM 227315) have both pelvic- and anal-fin hooks, while *Bryconamericus deuterodonoides* Schultz (USNM 121436) lacks such hooks. *Landonia latidens* also lacks bony hooks in the anal and pelvic fins of sexually mature males. *Phenacobrycon henni* has anal-fin hooks but no pelvic-fin hooks in mature males. If, for example, *Landonia latidens* is the sister taxon of the Xenurobryconini, absence of pelvic-fin hooks would be primitive for the group and for *Argopleura.* If the sister group of the Xenurobryconini occurs in *Bryconamericus* rather than in other so-called glandulocaudines, the absence of pelvic-fin hooks in *Argopleura* might be either primitive or derived. Since the exact outgroups for the Xenurobryconii are unknown, we cannot evaluate whether presence or absence of pelvic-fin hooks is derived. Therefore we are unable to use this character at this time.

The remaining seven possible subgroup A characters are reductive: loss of the adipose fin, reduction from seven to six branched pelvic-fin rays, and various laterosensory canal reductions, including loss of the pterotic canal, the supratemporal canal in the parietal bone, the extrascapular ossification, the supracleithral canal, and one or more circumorbital bones. All of these losses characterize *Iotabrycon.* However, the primitive state for each of these features is present in some subgroup B species. An adipose fin is present in some species of each subgroup B genus. *Xenurobrycon pteropus* (based on two known specimens) and *Scopaeocharax* species have seven branched pelvic-fin rays. Pterotic and supracleithral canals are present in one or more *Xenurobrycon* species and in some *Scopaeocharax* species. The remaining canal elements are present only in these same *Scopaeocharax* species. For most of these characters, it is more parsimonious to assume that the losses characterize subgroup A and presence of the primitive state in some members of the subgroup indicates a reversal. However, the absence of the adipose fin and reduction to six pelvic-fin rays may be explained as simply by independent loss in each genus. (Since we lack information on relationships within each genus, all these parsimony assessments assume loss or reappearance of a feature occurred only once within a genus.)

While the common assumption has been that the loss of a feature is more likely than its reappearance, this assumption has seldom been tested. Moreover, the presence or absence of laterosensory canal features is correlated with adult body size, not only in characids (for which see Weitzman and Fink, 1983:345–346, 391–394) but in teleosts generally. Reexpression of primitive states may be carried along with subsequent evolution of a slightly larger body size. Truncation of developmental sequences related to body size reduction does not necessarily imply loss of the genetic program for morphological expression beyond the truncated state. *Scopaeocharax rhinodus* and similar but undescribed species attain the largest body size of any subgroup A species, and it is these *Scopaeocharax* species that alone in subgroup A exhibit the primitive state for three of these features. On the other hand, expression of the primitive and derived states among the other subgroup A species does not seem correlated with the small differences in adult body size. For example, *Scopaeocharax atopodus* attains a larger body size (as far as is known) than *Xenurobrycon heterodon* or *X. pteropus* and yet exhibits more of these loss features (including absence of the adipose fin, present in *X. pteropus*; absence of the pterotic canal, present in both *X. pteropus* and *X. heterodon*; and absence of the supracleithrum canal, present in *X. heterodon*).

In sum, while these seven reductive features might be interpreted as synapomorphies of subgroup A, the support they give the group is ambiguous. Preferring the hypothesis that *Scopaeocharax* exhibits the primitive state of at least some of these characters as a result of reversal requires the assumption that regain of such features, due perhaps to simple changes in regulatory genes, is as likely as loss (i.e., that loss and reacquisition of such features can be weighted equally in a parsimony assessment). Whether such an assumption can be defended is not clear. At this point it might seem just as plausible that one or more *Scopaeocharax* species simply retained the primitive state in at least some of these features and that reductions occurred independently in one or more species of *Iotabrycon, Xenurobrycon, Tyttocharax,* and, in some cases, *Scopaeocharax*.

An alternative hypothesis of relationships of one subgroup A genus, *Iotabrycon,* was proposed by Roberts (1973). Roberts (1973:489, 491, 512) thought it probable that the monotypic *Landonia, Phenacobrycon,* and *Iotabrycon* were one another's closest relatives and had a *Bryconamericus*-like ancestor. Roberts (1973:489) found that the "osteological characters they [the Guayas glandulocaudines] share also occur in *Bryconamericus, Astyanax* and probably many other generalized characids." Roberts (1973:512) further stated, "I have not been able to find any specialized osteological characters which would serve to identify *Iotabrycon, Phenacobrycon,* and *Landonia* as a closely related group." He made no attempt to explore the relationships of *Iotabrycon* with other glandulocaudines but did remark (Roberts, 1973:489) that "a close relationship, especially to *Argopleura* cannot be ruled out." We were also unable to corroborate placement of *Iotabrycon* with *Landonia* and/or *Phenacobrycon* and our evidence contradicts such a relationship.

Eight autopomorphies diagnose *Iotabrycon.* The first five (apomorphies 19–23) are innovative features associated with the caudal-fin structure in the male. The remaining three (apomorphies 24–26) are reductive characters. One of these, loss of a process of the anguloarticular bone, suggests an alternative generic grouping, placing *Iotabrycon* with *Tyttocharax*. This grouping is not supported by other characters.

Subgroup B (*Xenurobrycon, Scopaeocharax,* and *Tyttocharax*) is the best corroborated group, having 20 synapomorphies, of which 18 are unique and innovative rather than reductive. Eleven of these (apomorphies 27–37) involve parts of the complex active muscular pheromone pump in males, while three (apomorphies 40–42) are male secondary sexual characters associated with the pelvic bones and fins. Features associated with the teeth (apomorphies 44–46) appear to be innovations found in both sexes and are probably associated with diet and methods of capturing prey. We found two reductive characters at the subgroup B level, 18 or fewer anal-fin rays (apomorphy 38) and an absence of the posterior cartilaginous process of the pelvic bone in both sexes (apomorphy 39). These are not sexually dimorphic and may be associated with small body size. However, one of the secondary sexual characteristics of the male pelvic girdle, the anterior position of that girdle, is in part also present in the females in a less derived form (apomorphies 41, 42).

All of the sexually mature males of the species of subgroup B have a few to numerous caudal-fin ray hooks (Figures 11–14) except *Xenurobrycon pteropus* and an undescribed species of *Tyttocharax*. Considering possible seasonal presence or absence of hooks described below for *Xenurobrycon heterodon* and for *Cheirodon affinis* by Fink and Weitzman (1974:22), we hesitate to conclude that hooks are absent in these species of subgroup B xenurobryconins. Even if they are absent, the most parsimonious cladogram indicates their absence to be a secondary loss.

Caudal-fin hooks are absent in specimens of the species of *Argopleura* and *Iotabrycon* examined (Figures 8–10). Thus the presence of such hooks may be a synapomorphy of subgroup B. However, many other glandulocaudines have caudal-fin hooks (for example Figures 17, 19). Some other characids also bear caudal-fin hooks (see Fink and Weitzman, 1974:8, fig. 3; and the discussions by Wiley and Collette, 1970:164; Roberts, 1973:513; and Collette, 1977:236–241). Although it is most parsimonious to assume that presence of hooks is a synapomorphy of subgroup B, this feature is so variable in characids that it lends only ambiguous support to the hypothesis of monophyly of the group and we have not included it in the apomorphy list.

We have found only one feature suggesting generic relationships in conflict with those corroborated by the 20 synapomorphies of subgroup B. That feature, loss of a lateral lamellar process on the anguloarticular bone, occurs in *Iotabrycon* (apomorphy 26) and *Tyttocharax* (apomorphy 71).

Xenurobrycon is corroborated by eight synapomorphies, all of them secondary sexual characters of the males. Four of these (apomorphies 47–50) are parts of the caudal pump apparatus and four (apomorphies 51–54) are pelvic girdle modifications. The only characters that could be interpreted as contradicting a hypothesis that the species of *Xenurobrycon* form a monophyletic lineage are the reduction to six branched pelvic-fin rays, and losses of the adipose fin, the pterotic laterosensory canal, and the supracleithral laterosensory canal. These features are discussed above under subgroup A.

The only possible synapomorphies we have discovered that could resolve relationships within *Xenurobrycon* are either reductive features, or a possible reversal: loss of an adipose fin and reduction to six branched pelvic-fin rays, shared by *X. macropus* and *X. heterodon*; loss of the supracleithral laterosensory canal, shared by *X. macropus* and *X. pteropus*; and reappearance of a partially developed pterotic laterosensory canal, shared by *X. pteropus* and *X. heterodon*. On the basis of this evidence, the *X. macropus*–*X. heterodon* grouping appears to receive slightly more support. (We note parenthetically that because our sample of *X. pteropus* is limited to two specimens, it is impossible to be certain that a count of seven branched rays is really characteristic of that species; an occasional specimen of *X. macropus* had a count of seven.) The most parsimonious cladogram, which includes all these features as well as the numbered apomorphies, however, requires that possession of only six branched pelvic-fin rays and absence of both a pterotic and a supracleithral canal be interpreted as synapomorphies of subgroup A and, therefore, as uninformative within *Xenurobrycon*. Based on this interpretation, reappearance of a pterotic canal is the only informative character and the *X. pteropus*–*X. heterodon* grouping should be preferred. We do not argue for such a preference here, for two related reasons. One, as discussed just above, it is not yet clear whether reversals are as likely as losses. Two, grouping *X. heterodon* with *X. macropus* adds only one step to the tree, requiring only an additional instance of reduction in the pterotic canal. In light of this, we are of the opinion that the parsimony criterion is not decisive in this instance and none of these hypotheses can be preferred as yet.

Subgroup C (*Scopaeocharax* and *Tyttocharax*) is supported by six synapomorphies. Five of these (apomorphies 55–59) are associated with the caudal pump; the other (apomorphy 60) is the nearly complete row of maxillary teeth in adult males. We find these synapomorphies quite clear morphologically. However, four other apomorphies suggest a relationship between *Tyttocharax* and *Xenurobrycon*.

These are as follows: In sexually mature males the membranes between the first, undivided ray of the pelvic fin and all the other rays except the inner two are broard to very broad, but the rays do not diverge broadly at their distal tips. Thus when the fin is extended and spread it forms an inverted, boat-shaped canopy (in Figures 72 and 73 the pelvic fins of *Tyttocharax madeirae* and *Xenurobrycon macropus* are drawn only slightly spread). In *Tyttocharax* the fin rays lie more or less parallel, but when the fin is spread widely the distal tips of the rays are seen to converge since the ray membrane is wider between the middle of the rays than the tips of the rays. In *Xenurobrycon macropus,* even in the folded fin, the distal tips of the fin rays converge. In other xenurobryconins, glandulocaudines, and characids the pelvic-fin rays gradually diverge from each other, do not have large amounts of membrane between the central portions of the fin rays, and do not have all the fin-ray tips converging when the fin is spread widely.

In sexually mature males the bases of most of the posterior five to eight anal-fin rays are the same size or larger than the anterior ray bases. (See Figure 75 of *Tyttocharax madeirae,* in which there is a progressive size increase posteriorly in the five penultimate rays; Figure 77 of *Xenurobrycon macropus*, in which all the ray bases are about the same size; and Figure 78 of *Xenurobrycon pteropus* in which all posterior ray bases are enlarged except the last two.) Furthermore, in sexually mature males the posterior 5 to 10 proximal radials of the anal fin are expanded in a sagittal plane, forming anything from a slightly flattened, expanded radial to a large, flat plate (see apomorphy 68). In all cases the posterior proximal radial is large and flattened. There is a fairly close correspondence between the proximal radials and the ray bases, both in numbers of enlarged elements and degree of enlargement (compare Figures 75, 77, 78).

In other xenurobryconins, glandulocaudines, and nearly all other characids there is a progressive gradual decrease in the size of the bases of the posterior anal-fin rays, correlated with decreased length of the posterior anal-fin rays. Similarly, the posterior radials remain slender rods, except for the posterior radial, which may be slightly expanded (Figure 76). In one glandulocaudine, *Corynopoma riisei,* there is a relatively small degree of expansion in two or three of the posterior proximal radials. The most parsimonious hypothesis indicates that this occurrence is independent of the expansion in *Tyttocharax* and *Xenurobrycon*.

These anal-fin features appear correlated with the posterior location of the large anal-fin hooks in species of *Tyttocharax* (apomorphy 67; Figure 41). The same is not true of *Xenurobrycon*; hooks are relatively posterior and large in *X. pteropus* (Figure 43), but not in *X. macropus* (Figure 42) or *X. heterodon*. The lack of derived similarity between *Tyttocharax* and *Xenurobrycon* species in the details of these anal-fin hooks (described further under apomorphies 67 and 68) fails to corroborate the hypothesis that the similarities are synapomorphies for a group comprised of the two genera.

A pectoral girdle apomorphy is shared by *Tyttocharax* and *Xenurobrycon*. The dorsal ramus of the supracleithrum is narrow, curved anteriorly, and attached to the pterotic bone near the anteroventral corner of the opening of the posttemporal fossa (Figures 54, 55). Other xenurobryconins (Figures 51–53, 56) and most other characids have the dorsal ramus of the supracleithrum extending more directly dorsally and attached by ligaments to the medial face of the ventral portion of the posttemporal bone. Occasionally in *Iotabrycon* the posttemporal and supracleithrum are fused. The usual characid condition is illustrated in Figures 57 and 58 of *Astyanax mexicanus*. In some characids the supracleithrum and associated structures are reduced but the supracleithrum is not curved anteriorly as in *Tyttocharax* and *Xenurobrycon*. (For example, see figures 6–8, 12, 13, 14, and 18 in Weitzman and Fink, 1983:353–355, of species of *Paracheirodon*, *Hemigrammus*, *Axelrodia*, *Brittanichthys*, and *Elachocharax* respectively.) The postocular region of *Klausewitzia aphanes* Weitzman and Kanazawa (1977:151) has a reduced dorsal ramus of the supracleithrum and a reduced posttemporal extending and curving anteriorly in association with the pterotic bone. Compare figure 17 of *Klausewitzia aphanes* in Weitzman and Fink (1983:356) with our Figure 54 of *Tyttocharax madeirae*. In our opinion the similarity between *Xenurobrycon* and *Tyttocharax* on the one hand and *Klausewitzia* and the other characids listed on the other is superficial. In any case, it is most parsimonious to accept that the similarity is derived independently in *Xenurobrycon*, in *Tyttocharax*, and in various other characids.

The final character, a loss of the epioccipital bridge in all specimens of *Xenurobrycon* and *Tyttocharax* examined, is a reductive feature associated with small size in characids. See Weitzman and Fink (1983:354). Parsimony indicates that this feature is not a synapomorphy of *Xenurobrycon* plus *Tyttocharax* (see historical survey of subgroup B, p. 44).

Of these four possible synapomorphies between *Xenurobrycon* and *Tyttocharax*, we find the anal fin morphology least convincing as a homology because of the lack of detailed similarity. The three other characters are more similar in detail but they are reductive characters common in small characids. The six characters indicating a relationship between *Scopaeocharax* and *Tyttocharax* are not very similar in detail but five of them appear to be innovative characters (character 56 is a reversal). Although the caudal characters at least may be associated with small size, none of the six features are reductive. Thus, the most parsimonious hypothesis, and the one preferred by us, groups *Tyttocharax* with *Scopaeocharax* rather than with *Xenurobrycon*.

If, however, one is willing to assume that none of the seven reductive features discussed above as possible synapomorphies of subgroup A could have undergone reversal, then three additional reductive features could be construed as synapomorphies for *Tyttocharax* and *Xenurobrycon*: loss of the supratemporal canal, of the extrascapular, and of the sixth infraorbital bone. Under such an assumption, this grouping would share seven derived features, one more than the number shared by *Tyttocharax* and *Scopaeocharax*, and so would be the preferred grouping. We do not see how such an assumption can be defined at this time.

Mahnert and Géry (1984, table 3) listed two characters that contradict the monophyly of subgroup C: loss of the adipose fin, present in *Xenurobrycon macropus* and *Scopaeocharax atopodus*, and reduction to six branched rays in the pelvic fin, present in *X. macropus* and *Tyttocharax madeirae*. Both of these features are discussed under subgroup A. The pelvic-fin character, also present in *X. heterodon* (and *Iotabrycon praecox*), might be interpreted as supporting a *Xenurobrycon–Tyttocharax* grouping, although one would also have to postulate a reversal to seven rays in *X. pteropus* (based on our limited sample of that species). Even if this feature is added to the four features shared by *Xenurobrycon* and *Tyttocharax* discussed just above, subgroup C remains the better supported hypothesis.

Mahnert and Géry (1984, table 3) also listed four characters as corroborating *Tyttocharax* (= our subgroup C) as a monophyletic group. One of these, number of maxillary teeth, is approximately equivalent to our character 60 (nearly fully toothed maxilla). The other three characters, considered derived relative to the condition in *Xenurobrycon,* are an elongated maxilla, a greater number of mandibular teeth, and the more posterior position of the male anal-fin hooks. The polarity of the maxillary length is complex and in the discussion on page 63 we indicate why we have not used this as a character. We have not used the number of mandibular teeth as a synapomorphy pending an analysis of its variability among the species (several undescribed) of *Scopaeocharax* and *Tyttocharax.* The position of the anal-fin hooks does not seem to us to distinguish *Xenurobrycon* and subgroup C; in *X. pteropus* the hooks are positioned about the same as in *S. atopodus* (in which the hooks occur only to the tenth branched ray in the specimens we examined, rather than the thirteenth as reported by Mahnert and Géry). Absence of hooks on the large unbranched ray may be a subgroup C character, but since *Iotabrycon* and *Argopleura* lack such hooks it is more parsimonious to assume that the presence of such hooks in *Xenurobrycon* is the derived state.

Scopaeocharax is corroborated by six synapomorphies, two of which are secondary sexual characters in males (apomorphies 61 and 63). Apomorphy 62 is the position of the pelvic girdle in females. The other features, proximity of the pterosphenoid and parasphenoid bones in relation to the prootic, shape of the premaxilla, and a nearly complete row of maxillary teeth in the adults of both sexes, do not seem associated with reduction of body size. All these synapomorphies of *Scopaeocharax* appear to be innovations. The evidence we have found that contradicts the hypothesis that the species of *Scopaeocharax* form a monophyletic lineage consists of six of the reductive characters that are most parsimoniously explained as synapomorphies of subgroup A. Some *Scopaeocharax* species show the primitive condition for each of these reductive features (see p. 63 for discussion of possible subgroup A characters). If the primitive conditions in these species are interpreted as reversals, then three of the six reversals are unique to *Scopaeocharax rhinodus* and a similar undescribed species and offer no challenge to the monophyly of *Scopaeocharax.* The remaining three characters (all six characters if reversals are considered less likely than parallel reductions) are inconsistent with the monophyly of *Scopaeocharax*; i.e., in each case the derived state is shared by some *Scopaeocharax* species and one or more species of at least one other subgroup A genus. In order to accept a hypothesis of nonmonophyly of *Scopaeocharax,* however, one must not only assume that multiple parallelisms are more likely than reversals, but one must also assume that these six features are better indicators of relationship than the six innovative features unique to *Scopaeocharax* species among xenurobryconins (and in the case of apomorphy 65, unique among characids). However, if the other subgroup B genera are monophyletic and if subgroup B itself is monophyletic, then three of these reductive features cannot be uniquely derived, i.e., well correlated with phylogeny, even within the Xenurobryconini. In addition, as noted previously, these reductive features are correlated with size and exhibit homoplasy among other members of the Characidae (as well as other teleosts). Therefore, we prefer the hypothesis of monophyly of *Scopaeocharax* as better corroborated.

Mahnert and Géry (1984:512, fig. 18) suggested on the basis of three characters in their table 3, that *Scopaeocharax rhinodus* is more closely related to *Tyttocharax madeirae* than to *S. atopodus.* These are tooth and scale count characters and as used by Mahnert and Géry do not corroborate our six synapomorphies for *Scopaeocharax.* The first, the number of tooth rows in the premaxilla, is given as in "brush form" for *Tyttocharax madeirae,* in two rows for *Scopaeocharax atopodus,* and in three rows for *Scopaeocharax rhinodus. Xenurobrycon,* the outgroup, is said to have two tooth rows. Since *S. rhinodus* has the closest tooth-row number to the "brushlike" teeth of *T. madeirae, S. rhinodus* was suggested by Mahnert and Géry to be related to *T. madeirae.* We find premaxillary tooth rows difficult to distinguish clearly in these fishes. We have identified four to about eight premaxillary tooth rows in species of *Tyttocharax.* In large specimens of both *Scopaeocharax rhinodus* and *S. atopodus* (see Appendix 1 for largest specimens) we have been able to recognize at least three rows. It seems clear to us that an increase in premaxillary tooth row numbers beyond two could be used as a synapomorphy for subgroup C xenurobrycons and for *Tyttocharax* but that it does not show that *S. rhinodus* and *T. madeirae* are one another's closest relatives. We have not used premaxillary tooth-row numbers as a synapomorphy for these taxa pending a review of the species of *Scopaeocharax* and *Tyttocharax*.

The second character used by Mahnert and Géry (1984) is the premaxillary tooth number. They found about 8 to 9 (we found 7 to 10) in *Xenurobrycon macropus*, 14 in *Scopaeocharax rhinodus*, 7 in *Scopaeocharax atopodus*, and 20 to 25 in *Tyttocharax madeirae*. Again, because *Scopaeocharax rhinodus* had the number most closely approaching the high number in *Tyttocharax madeirae*, the two species were thought by Mahnert and Géry to be related. We have seen up to 8 premaxillary teeth in *S. atopodus* and 15 in *S. rhinodus*. This feature does seem to corroborate their hypothesis, but we note that the low count in *S. atopodus* may be due to the large size of the teeth and the narrowness of the premaxilla in that species (Figure 60), and thus may be secondary rather than primitive. In any case, we have not used this character pending a detailed analysis of the species in *Scopaeocharax* and *Tyttocharax*.

The third character used by Mahnert and Géry (1984) to relate *Scopaeocharax rhinodus* and *Tyttocharax madeirae* is a similar number of lateral-series scales, 35 to 37 and 35 to 36, respectively. This is contrasted with 32 to 34 for *Scopaeocharax atopodus* and 30 to 32 for *Xenurobrycon macropus*. We have not made scale counts for most of the various species of *Scopaeocharax* and *Tyttocharax* but note that lateral-series scales in three species of *Xenurobrycon* recorded here range from 32 to 35. Thus the taxa do not appear as distinct in this character as indicated by Mahnert and Géry, but information on additional species is needed. Pending a detailed analysis of the lateral-series scale counts in the species of *Scopaeocharax*, *Tyttocharax*, *Xenurobrycon*, and their outgroups, we have omitted this character from our analysis.

One character used by Mahnert and Géry (1984, table 3), high number of maxillary teeth, suggests to us that *Scopaeocharax rhinodus* is related to *S. atopodus* rather than to *Tyttocharax madeirae*. We have used this character stated in qualitative rather than quantitative terms as a synapomorphy for subgroup C (apomorphy 60).

According to our analysis, Mahnert and Géry (1984) applied the number of premaxillary tooth rows to the wrong taxa. The number of premaxillary teeth as analyzed by them may represent a homoplasy. Finally, their analysis of lateral-series scales is based on inadequate samples for the levels of relationship being considered.

Tyttocharax is corroborated by two secondary sexual characters (apomorphies 67 and 68), both associated with the posterior anal-fin hooks (Figure 41). Two other characters (apomorphies 69 and 70), a high number of teeth and tooth rows on the premaxilla and dentary, may show slight differences between the sexes, but the characters are clearly present in both sexes. The fifth character (apomorphy 71), an absence of the anguloarticular process in the lower jaw, is a character not necessarily associated with small size since many miniature characids have the process. Only loss of the adipose fin, shared by some *Tyttocharax* species with one or more species of every other subgroup A genus, contradicts the hypothesis of relationship suggested by these characters.

In summary, the data presented above corroborate the cladogram presented in Figure 79. This cladogram can be represented by a sequenced phylogenetic classification (Wiley, 1981:206). By convention, when there are three or more taxa of the same categorical rank that are not otherwise annotated, the order of names corresponds to branching sequence. Thus, the first taxon is recognized as the sister group to the following taxa of that rank, the second as the sister group to those following it, and so on. The resulting classification for the Xenurobryconini is as follows.

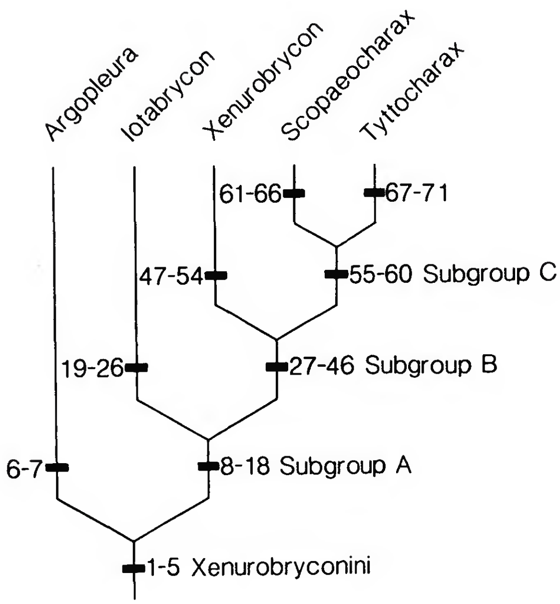


FIGURE 79.—Cladogram of the Xenurobryconini. Numbers correspond to apomorphies described in text.

Tribe Xenurobryconini
Argopleura
Iotabrycon
Xenurobrycon
Scopaeocharax
Tyttocharax

Xenurobryconin Distribution

Much has been written on areas of endemism within South America from the perspective of various biogeographic theories (see review by Weitzman and Weitzman, 1982). As noted by those authors, very little has been published on the interrelationships of those areas based on phylogenetic analyses of endemic fishes. Thus little evidence is available to judge how historical relationships of parts of South America have affected the variety of organisms inhabiting them. In order to contribute to future investigations into historical biogeographic patterns in South America, we present a distribution map and an area cladogram (Figures 80, 81).

Because our interest is in general patterns and explanations, we employ the "vicariance" method of Platnick and Nelson (1978) and Rosen (1978). In studying interrelationships among areas of endemism, only allopatric taxa are informative, because only they diagnose areas of endemism. Sympatry due to sympatric speciation should not be correlated historically with areas of endemism or have a general geographic explanation. Sympatric distributions due to dispersal or to range expansion following allopatric speciation may contain limited, hidden information about areas of endemism, but such information can only be extracted in the context of a corroborated cladogram of areas of endemism, to which the cladograms and distributions of the sympatric taxa can be "fitted."

Within the Xenurobryconini, there are only three allopatric taxa at the generic or suprageneric level: *Argopleura, Iotabrycon,* and subgroup B. Summaries of the collecting localities for these three taxa are mapped in Figure 80. Since all of these taxa are known from relatively few collections, these distributions must be viewed as sketchy estimates of the actual species ranges. Given this caveat, we can characterize the three areas as follows. The Magdalena area comprises the Magdalena basin (Río Magdalena and its tributaries) and the upper Río San Juan, northern and western drainages west of the eastern cordillera of the Andes. The Guayas area comprises the upper Guayas basin in southwestern Ecuador, west of the western cordillera. The third area, which we will simply term Eastern, comprises western and central parts of the Amazon basin and at least the middle and upper parts of the Paraguay-Paraná basin exclusive of the plateau region in Brazil above Sete Quedas.

These taxa, *Argopleura* (Magdalena area), *Iotabrycon* (Guayas areas), and subgroup B (Eastern), support the area cladogram illustrated in Figure 81.

Unfortunately, we know of no other cladograms or area cladograms which include all three of these areas. Since at least three areas are needed to test area cladograms, no tests can as yet be performed with the area cladogram of Figure 81.

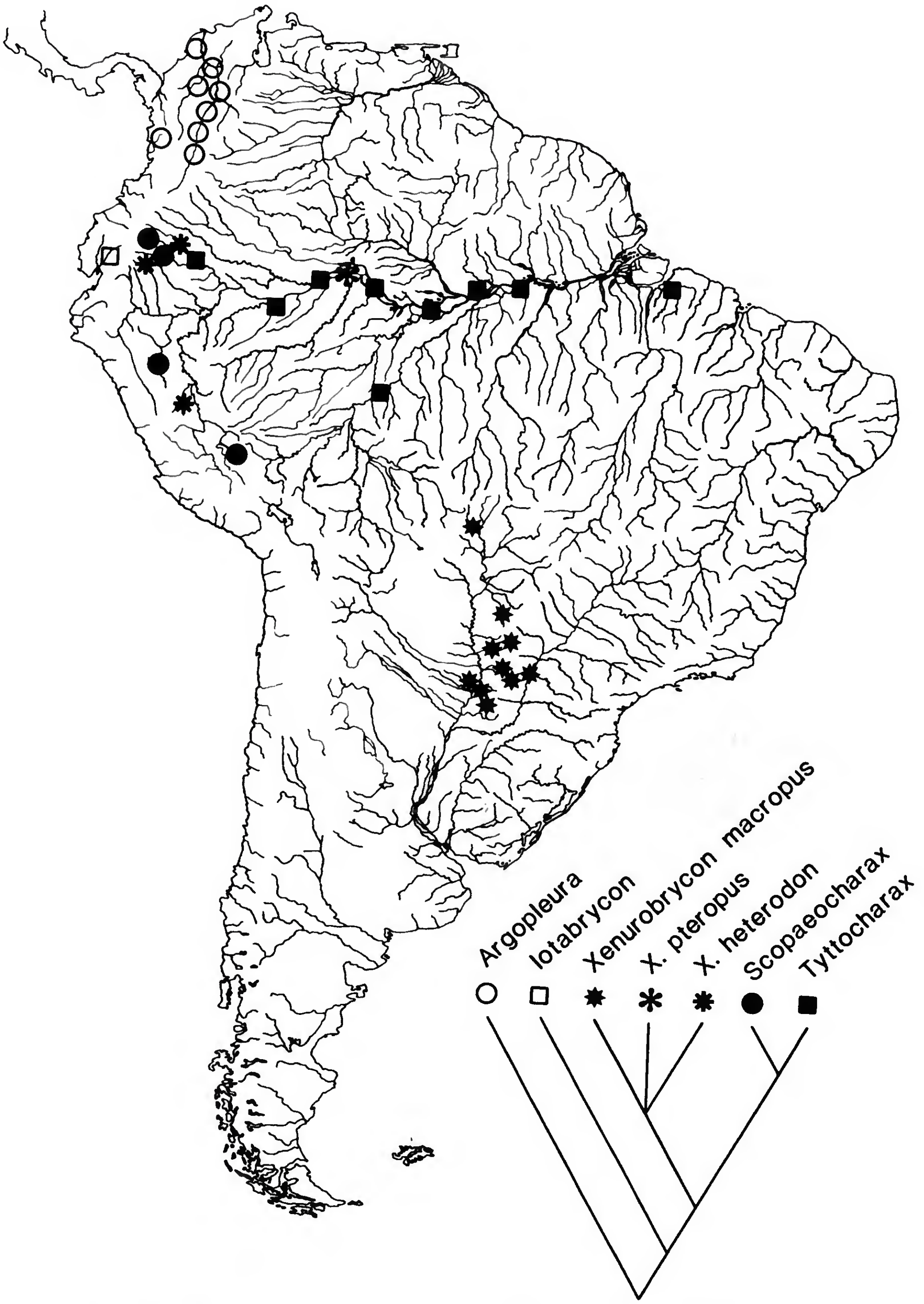


FIGURE 80.—Summary of known collecting localities of xenurobryconins.

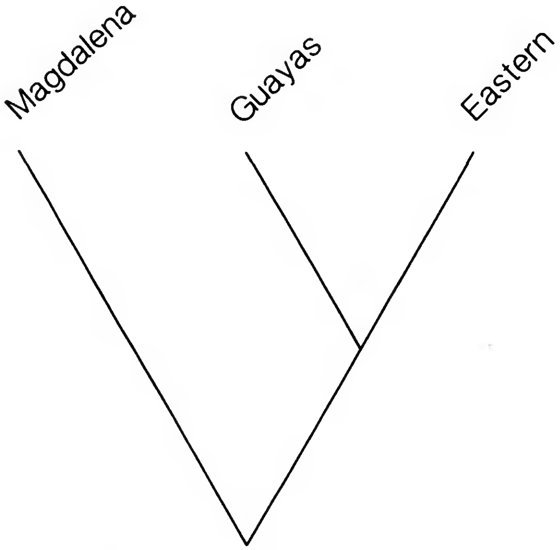


FIGURE 81.—Area cladogram supported by xenurobryconin taxa.

Key to Generic Groups and Genera

This key is based for the most part on characters derived from the apomorphy list. When appropriate, characters for which we could not hypothesize polarity have been used in the key.

1. If hypertrophied scales present in caudal region of sexually mature males then not part of lateral-line series (except for *Saccoderma* Schultz, 1944:314, considered a relative of *Cheirodon* and not a glandulocaudine; see Appendix 2 and Fink and Weitzman, 1974:33, fig. 26) or, if part of lateral-line series, then not forming part of the lateral wall of caudal pouch; parhypural and hypural 1 not fused . . . . non-xenurobryconin glandulocaudines

   Caudal region of sexually mature males with following features: one very large caudal pouch scale, which is either a lateral-line scale or in series with scales of lateral line; parhypural and hypural 1 fused to a single bony element (Xenurobryconini) 2

2. Lateral line complete; sexually mature males with a lateral-line tube in pouch scale; teeth of upper jaw multicuspid (one or two posterior teeth occasionally may be conical in juveniles); accessory pouch scale with elongate posterodorsal process medial to pouch scale (occasionally fused to pouch scale); caudal musculature of males relatively unmodified, interradialis, epaxialis, and hypaxialis muscles with insertions like those of other characiforms, not inserting on pouch scale (interradialis) or extending distally onto dorsal caudal-fin lobe (epaxialis and hypaxialis); adult size exceeding SL of 25 mm . . . . ***Argopleura***

Lateral line absent or incomplete, with up to seven anterior perforated scales; all or most teeth of upper jaw conical; accessory pouch scale without process medial to pouch scale; either hypertrophied interradialis muscles inserting on large pouch scale or combined epaxialis and hypaxialis muscle bundle hypertrophied and inserting distally on dorsal caudal-fin lobe; adult size less than about SL 25 mm, sometimes sexually mature at about SL 12.5 mm (Subgroup A) 3

3. Predorsal area of body without scales; maxilla toothless; pouch scale of sexually mature males with elongate ventral posterior process, which equals or surpasses length of main fimbriate field of scale; combined large epaxialis and hypaxialis muscle bundle inserting distally on dorsal caudal-fin lobe in sexually mature males; caudal interradialis muscles originating from 11th ray never fan-shaped or inserting on pouch scale; proximal end of principal caudal-fin ray 11 not enlarged or unciform in shape .... ***Iotabrycon***

Predorsal area of body fully scaled; maxilla toothed along almost half or much more than half of its free ventral border; pouch scale of sexually mature males without a long ventral posterior process; no large muscle bundle of epaxialis and hypaxialis; caudal interradialis muscles of 11th ray hypertrophied with a fan-shaped portion inserting distally on pouch scale; proximal end of principal caudal-fin ray 11 enlarged, unciform in shape, and serving as origin for hypertrophied interradialis muscles (Subgroup B) 4

4. Maxilla of adults with approximately anterior half of its free border toothed; pouch scale of sexually mature males without a prominent anteroventral notch; pelvic fin of sexually mature males over one-third of SL .... ***Xenurobrycon***

Maxilla of adults three-fourths to fully toothed along its free ventral border; pouch scale of sexually mature males with a prominent anteroventral notch; pelvic fin of sexually mature males less than one-third of SL (Subgroup C) 5

5. Adults with no more than a few exserted teeth on premaxilla and dentary; maxilla long, extending well posterior to anterior border of eye in adults of both sexes; maxilla with a complete or nearly complete row of teeth along its ventral free border; anal fin of sexually mature males with hooks distributed more or less evenly over most of anterior, middle, and sometimes also on nearly all posterior anal-fin rays; dorsal margin of parasphenoid and ventral margin of pterosphenoid in contact or close proximity in lateral view of orbit ....
.... ***Scopaeocharax,*** new genus

Adults with many exserted teeth on premaxilla and dentary; maxilla short, extending to anterior border of eye but not beyond in adults of both sexes; anterior three-fourths of free ventral maxillary border with teeth in sexually mature males; anal-fin hooks of sexually mature males confined to posterior six to eight rays; parasphenoid and pterosphenoid well separated by prootic in lateral view of orbit ...... ***Tyttocharax***

The Species of *Xenurobrycon*

The following account of the species of *Xenurobrycon* is presented without a phylogenetic analysis. Accounts of the species of *Scopaeocharax* and *Tyttocharax* are being prepared by the senior author and a phylogenetic analysis of all known species of subgroup C xenurobryconins will be attempted at that time.

Artificial Key to the Species of *Xenurobrycon*

1. Jaw teeth unicuspid, bicuspid, and tricuspid; anterior, large teeth of lower jaw especially likely to be tricuspid (Figure 65); pouch scale in sexually mature males approximately teardrop-shaped, with posterior process elongate and terminating in a relatively acute angle [Figure 30] .... ***Xenurobrycon heterodon***, new species

   Jaw teeth all conical (Figures 63, 64); posterior process of pouch scale in sexually mature males either elongate or short but with a blunt termination [Figures 28, 29] 2
2. Adipose fin absent; sexually mature males with semicircular flange-like process on principal caudal-fin ray 18 near pouch scale [Figure 11]; in sexually mature males, posterior anal-fin hooks slender, no larger than anterior hooks [Figure 42] .... ***Xenurobrycon macropus***

   Adipose fin present; sexually mature males without semicircular flange-like process on principal caudal-fin ray 18; in sexually mature males eighth to eleventh or twelfth principal anal-fin rays each with a stout large hook which is distinctly larger than more anterior hooks [Figure 43] .... ***Xenurobrycon pteropus***, new species

Xenurobrycon macropus Myers and P. de Miranda-Ribeiro

FIGURES 3, 11, 25, 28, 31, 34*d*, 37*a*, 42, 47, 63, 64*a*, 67, 73, 77

Xenurobrycon macropus Myers and P. de Miranda-Ribeiro, 1945:5, fig. 1 [type locality: Brazil, Mato Grosso, Rio Bodoquena].—Fowler, 1951:419, fig. 465 [listed].—Myers and Böhlke, 1956:10 [listed, discussion of relationships].—Böhlke, 1958b:319 [listed, discussion of relationships].—Géry, 1977:363 [listed].—Mahnert and Géry, 1984:498 [redescription, osteology, discussion of relationships].

MATERIAL EXAMINED.—BRAZIL: MNRJ 4124, holotype, male, SL 16.0 mm; MNRJ 4124, paratype, female, SL 17.8 mm; MNRJ 4125, paratypes, 14 adults, SL 15.4–17.8 mm; and CAS(SU)40764, paratypes, 1 male, 1 female, SL 16.3, 17.6 mm; Mato Grosso: Rio Bodoquena, 19°10'S, 56°55'W, Paulo de Miranda-Ribeiro, Dec 1941. MZUSP 13966-69, 2 males, 2 females, SL 14.4–15.6 mm, Paraná: mouth of Rio Itacoty and Rio Miguaçu below Sete Quedas waterfalls of Rio Paraná, 24°25'S, 54°20'W, CETESB, November 1977. MZUSP (uncataloged), 13 immatures to adults, SL 12.0–15.8 mm, Mato Grosso: Muniçípio de Cáçeres, Rio Jaurú, (precise locality not recorded but mouth of Rio Jaurú into Rio Paraguay at about 16°17'S, 57°47'W, CEPIPAM, 26 Mar 1977.

PARAGUAY: USNM 219381, 1 male and 1 female, SL 15.4, 17.1 mm; and USNM 219382, stained, 1 female, 1 male, SL 14.4, 15.2 mm; Paraguari: Lago Ypacarai, 25°17'S, 57°20'W, J. Talbot, 3 Dec 1976. UMMZ 205412, 8 immatures to adults, SL 14.4–14.8 mm; La Cordillera: Arroyo Tobati, tributary to Rio Piribebuy about 1 km east of Tobati, 25°16.9′S, 57°3.3′W, J.N. Taylor, T.W. Grimshaw, R.M. Myers, 4 Jun 1979. UMMZ 205413, 25 immatures to adults, SL 13.8–14.2 mm; Paraguari: Arroyo Caañabe at 80 km on Route 1 at bridge, about 13 km south of Paraguari, 25°45′S, 57°11.7′W, R.M. Bailey, J.N. Taylor, T.W. Grimshaw, 19 Jun 1979. UMMZ 205414, 42 immatures to adults, SL 13.3–19.2 mm; Canendiyu: Arroyo Curimbaty about 15.6 km west by southwest, dirt road from Curuguaty, 24°31.1′S, 55°43.5′W, R.M. Bailey, J.N. Taylor, T.W. Grimshaw, 6 Jul 1979. UMMZ 205416, 32 adults, SL 16.6–19.8 mm; Canendiyu: Rio Jejui, tributary to Rio Jejui-Guazu about 41 km north of Curuguaty and 2 km south of Ybatimi, 24°8.2′S, 55°37.8′W, R.M. Bailey, J.N. Taylor, 7 Jul 1979. UMMZ 205419, 13 immatures and adults, SL 13.9–17.9 mm; San Pedro: Rio Corrientes and adjacent flood pool about 32.4 km west of turnoff to Curuguaty (and northeast of Mbutuy intersection), 24°22.9′S, 55°56.4′W, T.W. Grimshaw, R.M. Myers, 21 Jul 1979. UMMZ 205421, 2 immatures, SL 13.5, 15.3 mm; Concepcion: Rio Aquidaban at Paso Horqueta, swamp and pond within 300 m of road, about 24 km north by northwest of Loreto, 23°3.8′S, 57°23.4′W, J.N. Taylor, G.R. Smith, B. Smith, E. Koon, R.M. Myers, 6 Sep 1979. UMMZ 205422, 3 adults, SL 16.0–17.0 mm; San Pedro: south bank of Rio Ypane at bridge on dirt road 52.7 km south of Yby-Yau, 23°27.3′S, 56°31.2′W, J.N. Taylor, G.R. Smith, B. Smith, E. Koon, R.M. Myers, 11 Sep 1979. UMMZ 205423, 1 adult, SL 19.7 mm; Caaguazu: at bridge over Rio Tebucuary-mi about 20 km south of Coronel Oviedo on paved highway to Villarica, 25°37.6′S, 56°28.2′W, J.N. Taylor, G.R. Smith, B. Smith, E. Koon, R.M. Myers, 12 Sep 1979. UMMZ 205484, 1 male, 6 females (including 1 stained), SL 14.5–16.6 mm; Central: bridge over stream 7.0 km approximately east of Luque on dirt road to Aregua, 25°18.5′S, 57°22.8′W, J.N. Taylor, T.W. Grimshaw, G.K. Creighton, 17 May 1979. UMMZ 206422, 1 female, SL ~17.0 mm (damaged); Canendiyu: roadside swamp at bridge on dirt road about 1.3 km west of Salto del Guaira, 24°2.2′S, 54°19.2′W, J.N. Taylor, T.W. Grimshaw, G.K. Creighton, 13 Jul 1979. UMMZ 206314, 1 female, 1 male, SL 16.4, 18.2 mm; Canendiyu: Arroyo Itandey, tributary to Arroyo Carimbatay, about 7.6 km west southwest of Curuguaty by dirt road, 24°30.5′S, 55°40.2′W, R.M. Bailey, J.N. Taylor, T.W. Grimshaw, et al., 6 Jul 1979. UMMZ 206535, 7 immatures to adults, SL 15.5–16.8 mm, Canendiyu: small stream about 5.3 km by dirt road north northwest of Curuguaty, 24°25.1′S, 55°40.8′W, J.N. Taylor, T.W. Grimshaw, G.K. Creighton, 19 Jul 1979. UMMZ 206729, 7 males, 5 females, SL 15.5–18.9 mm; Concepcion: Arroyo Piky at bridge on Route 5 about 47 km west southwest of Pedro Juan Caballero, 22°42′S, 56°12.6′W, J.N. Taylor, T.W. Grimshaw, R.M. Myers, 24 Jul 1979. USNM 212549, 2 adults, SL 14.9, 16.6 mm; Presidente Hayes: pond about 15 by 30 m, near trans Chaco highway about 50 km north of Asuncion and 4 km north of Benjamin Aceval, about 24°52′S, 57°35′W, L. Naylor, F. Davidson, 1 Nov 1981.

Mahnert and Géry (1984:498, 508) list and discuss seven other Paraguayan localities which are in the same general region as the Paraguayan localities listed above.

DIAGNOSIS.—Premaxilla with single row of 6 to 10 conical teeth (Figures 63, 64). Maxilla with single row of 4 to 8 conical teeth. Dentary with single row of 8 to 14 conical teeth. Adipose fin absent. Adult males with following sexually dimorphic features: pouch scale shaped as illustrated in Figure 28, approximately rounded but with a very short, blunt protuberance posteriorly. Eighteenth principal caudal-fin ray (counting ventrally from dorsal principal caudal-fin ray) bearing thin, flat bilateral lamellae with rounded distal edges; these projections situated near ventral border of pouch scale. Each projection formed of two ventrolaterally expanded fin-ray segments fused in their expanded portions. Developing males with each ray half bearing a low ventrolateral ridge in this region, each ridge including at least two ray segments. Bony hooks present on large unbranched and 9 anterior branched anal-fin rays.

DESCRIPTION.—Tables 1 and 2 present morphometrics and meristics for four population samples; holotype given separately. Measurements are given separately for males and females for four characters. Body moderately elongate, sides compressed, greatest depth about midway between nape and dorsal-fin origin. Predorsal body profile gently convex to tip of snout. Body profile slightly elevated at dorsal-fin origin, slightly concave along dorsal-fin base, and nearly straight to origin of dorsal procurrent caudal-fin rays. Dorsal fin nearer to caudal-fin base than to snout tip. Ventral body profile gently convex from anterior lower jaw tip to pelvic-fin origin, slighty concave in region of pelvic-fin insertion. Body profile between pelvic-fin insertion and anal-fin origin slightly convex in males, slightly concave in females. Profile gently concave along anal-fin base and nearly straight from posterior termination of anal-fin base to origin of ventral procurrent caudal-fin rays.

Head and snout moderately elongate. Lower jaw protruding slightly beyond jaw or jaws equal. Mouth angled anterodorsally from mandibular joint to snout tip. Maxillary bone extending posteriorly approximately to a point on a vertical line drawn ventrally from anterior border of eye.

Dorsal-fin rays ii,7 in most specimens; branched ray count varies somewhat (Tables 1, 2) (last ray not split to its base). Adipose fin absent. Anal-fin rays iii,13 in most specimens; branched ray count varies (Tables 1, 2). Posterior anal-fin ray split to its base (Figures 42, 77). Anal fin with a strongly lobed anterior portion in males, lobe less developed in females. (Compare male and female in Figure 3; see also Tables 1, 2.) Anal fin of sexually mature males with bilateral antrorse bony hooks on largest anterior unbranched ray and anterior nine branched rays (Figure 42). Almost always one hook per segment. Anterior rays with largest number of hooks; progressively fewer hooks posteriorly. Number of hooks per ray ranging from a maximum of 10 anteriorly to 4 on posterior rays of anal-fin lobe, and 4 to 2 on rays posterior to lobe. Female without bony hooks.

Pectoral-fin rays i,6 to i,9, usually i,8 (Tables 1, 2). Distal tips of pectoral-fin rays extending posterior to pelvic-fin origin in females and well beyond that point in males due to anterior position in males of pelvic-fin origin. Actual pectoral-fin length about equal in both sexes (see p. 84, sexual dimorphism).

Pelvic-fin rays i,6 in nearly all specimens (Tables 1, 2). Pelvic fin sexually dimorphic, elongate in males (Figures 3, 73; Tables 1, 2). Pelvic-fin origin much nearer pectoral-fin origin than anal-fin origin in males, about equidistant between pectoral-fin origin and anal-fin origin in females. (See Tables 1, 2 for comparative ratios presented as percentages.) Pelvic-fin rays of females not elongate as in males and without hooks, similar to pelvic-fin rays of most female glandulocaudine characids. Pelvic-fin rays of males arched dorsally when folded against body (Figure 3). Membranes of pelvic fin in males broad between all but sixth and seventh fin rays, which are closely bound together along their entire length. Interradial membranes between third through sixth rays especially broad. All fin rays closely bound to adjacent rays at their distal ends by connective tissue and skin. When pelvic fin is expanded with forceps it forms an inverted boat-shaped structure or an "umbrella-like canopy" as noted by Myers and Miranda-Ribeiro (1945:3).

Pelvic-fin rays of males with unpaired ventral bony hooks (Figure 73). Anterior ray bears hooks along nearly its entire length; sixth and seventh rays (closely bound) bear hooks along most of their lengths; rays in middle area of fin have fewer hooks with fourth and fifth rays bearing hooks only along distal third. Hooks occur on all branches of branched rays. On all rays, more proximal hook-bearing segments usually bear 1 hook per segment, intermediate segments 2, and distal or penultimate 1 to 3 segments bear 3 hooks per segment. Anterior ray with 1 hook per segment along most of its length; remaining rays have very few (1 to 3) segments with 1 hook per segment. On each ray, hooks largest near middle of hook-bearing portion of ray; largest hooks of fin on anterior ray. On all rays more proximal hooks more antrorse, and more distal hooks project at right angles from ray segments. Hook counts on cleared and stained specimen from Lago Ypacarai, Paraguay, USNM 219381, as follows: anterior ray, unbranched, bears 34 mostly antrorse hooks distributed on about 21 ray segments, with 7 or 8 hooks on long basal segment and 1 to 3 hooks on more distal segments. Second ray, branched, bears about 56 slightly antrorse hooks, with unbranched portion bearing about 3 hooks, lateral branch about 12 hooks, and medial branch about 31 hooks. Third ray with about 15 slightly antrorse hooks on unbranched portion, about 10 slightly antrorse hooks on lateral branch, and about 24 slightly antrorse to nonantrorse hooks on medial branch. Fourth ray with smaller hooks, about 18 slightly antrorse hooks on unbranched portion, about 6 slightly antrorse hooks on lateral branch, and about 14 mostly nonantrorse hooks on medial branch. Fifth, sixth, and seventh rays unbranched; fifth ray bears about 30 antrorse hooks on about 15 segments, sixth ray abut 44 mostly antrorse hooks on about half as many segments, and seventh ray about 32 mostly antrorse hooks on about 17 segments.

Pelvic girdles of males large, anterior in position, and separated from each other posteriorly (Figure 37*a*; compare also snout to pelvic fin distances in males and females in Tables 1, 2). Anterior processes of pelvic bones almost in contact and extending to a point medial and slightly anteroventral to divergent posteroventral borders of coracoid bones of pectoral girdles. Lateral process of each pelvic bone positioned just posteroventral to ventral tip of anterior pleural rib. Posterior processes separated from each other in alizarin specimen by about 1.2 mm or a distance more than one-third of length of pelvic bone; anterior and posterior projections of posterior processes, present in most characids, very reduced. On each pelvic bone a large ventral flange extends from lateral process to point near midlength of medial pelvic bone border. Medial pelvic radial platelike and laterally elongate, closely bound to girdle so that little movement of radial is possible.

Pelvic girdle of female like that of most female glandulocaudines except that anterior and posterior projections of posterior process completely absent. Pelvic bones adjacent at midline. Anterior process distant from coracoid bone of pectoral girdle, lying just posteroventral to ventral tip of second rib; lateral process ventral to ventral tip of fourth rib.

Caudal fin with principal rays 10/9 in all specimens. Caudal fin of females, as in most other characids, similar to that of *Brycon* (Figure 21), but with 2 epurals instead of 3. Caudal fin of sexually mature males highly modified (Figures 11, 12, 25, 28, 47, 67). Principal caudal-fin rays 10/9 but rays so modified that conformance to this count is not easily recognizable in specimens not cleared and stained. Bony spines or hooks present on dorsal 8 or 9 and ventral 3 principal caudal-fin rays (Figure 11). These hooks usually distributed bilaterally with one bilateral pair per fin-ray segment. Hooks on dorsal lobe usually restricted to ventral borders of fin rays, and to ventral branches in branched areas of rays. Dorsal four principal caudal-fin rays with antrorse hooks, fifth ray with hooks directed ventrally, and sixth through eighth or ninth rays with larger, retrorse hooks. Hooks on ventral lobe antrorse and usually restricted to dorsal borders of fin rays and to dorsal branches in branched areas of rays. Largest procurrent ray of ventral lobe sometimes with an antrorse hook on its dorsal border. Hook counts for principal rays as follows: in dorsal lobe, first ray (unbranched) with 11 to 14 hooks, second ray with 9 to 13 hooks, third with 9 to 11, fourth with 4 to 7, fifth with 3 to 5, sixth with 4 to 7, seventh with 4 to 6, eighth with 1 to 6, ninth sometimes with 1 hook. In ventral lobe, seventeenth principal ray with 3 to 5 hooks, eighteenth with 4 to 9, and nineteenth with 8 to 12.

Table 1.—Morphometrics and meristics of *Xenurobrycon macropus.*

Character	Brazil, Rio Bodoquena[1]								Paraguay, Arroyo Curimbaty[2]						
			Range			95% Confidence limits[3]				Range			95% Confidence limits[3]		
	Holotype	n	low	high	$\bar{x}$	L_1	L_2	SD	n	low	high	$\bar{x}$	L_1	L_2	SD
Standard length (mm)	16.0	17	15.4	17.8	16.8			0.829	36	13.3	19.2	16.2			1.360
PERCENTAGE OF STANDARD LENGTH															
Greatest body depth	27.5	17	23.6	30.4	27.5	26.981	28.083		36	21.5	28.4	25.5	25.165	25.835	
Depth at dorsal-fin origin	25.6	17	23.6	27.3	25.5	25.169	25.831		36	21.3	27.7	23.9	23.588	24.212	
Snout to dorsal-fin origin	61.3	17	59.6	64.3	61.8	61.380	62.220		36	58.3	63.4	61.1	60.849	61.351	
Snout to pectoral-fin origin	23.1	17	22.6	26.0	23.9	23.596	24.204		36	21.7	26.3	23.3	23.083	23.517	
Snout to pelvic-fin origin ♂	33.8	6	32.3	36.4	34.4	33.615	35.385		13	30.1	39.1	33.4	32.779	34.021	
Snout to pelvic-fin origin ♀	–	11	42.2	46.9	44.6	44.069	45.131		22	39.6	45.1	42.3	41.963	42.637	
Snout to anal-fin origin	58.1	17	58.1	65.8	62.7	62.144	63.255		36	56.7	63.6	59.3	59.027	59.573	
Caudal peduncle depth ♂	14.4	6	13.5	15.6	14.6	14.019	15.182		13	11.2	13.5	12.4	12.062	12.738	
Caudal peduncle depth ♀	–	11	11.6	12.4	11.9	11.712	12.088		23	9.7	12.6	10.8	10.570	11.030	
Caudal peduncle length	19.4	17	19.4	24.2	21.7	21.359	22.041		36	19.8	26.3	22.3	22.030	22.570	
Pectoral-fin length	23.8	16	18.4	26.6	21.6	20.875	22.325		35	18.2	22.5	20.7	20.455	20.945	
Pelvic-fin length ♂	40.6	6	36.7	40.9	39.5	38.556	40.444		13	30.2	40.7	36.6	35.070	38.130	
Pelvic-fin length ♀	–	11	11.8	13.6	12.6	12.337	12.863		21	11.1	15.4	12.5	12.150	12.850	
Dorsal-fin base length	8.4	17	6.4	8.5	7.5	7.168	7.832		36	6.4	9.4	8.1	7.889	8.311	
Longest dorsal-fin ray length	23.1	17	18.0	25.3	21.3	20.610	21.991		34	20.0	24.8	22.3	21.981	22.619	
Anal-fin base length	19.4	17	17.5	21.8	19.1	18.702	19.498		36	18.8	22.5	20.4	20.142	20.658	
Anal-fin lobe length ♂	24.4	6	24.1	26.1	25.0	24.403	25.597		13	20.5	25.3	22.6	21.965	23.235	
Anal-fin lobe length ♀	–	11	16.6	21.0	17.9	17.353	18.447		19	17.4	22.7	19.1	18.640	19.560	
Bony head length	22.5	17	20.2	24.7	21.8	21.389	22.211		36	20.8	24.4	22.6	22.383	22.817	

	PERCENTAGE OF BONY HEAD LENGTH														
Horizontal eye diameter	41.7	17	38.5	44.4	41.7	41.196	42.204		36	37.8	45.7	42.0	41.615	42.385	
Snout length	20.8	17	16.9	21.1	19.0	18.557	19.443		36	17.4	22.9	20.0	19.710	20.290	
Least width interorbital	38.9	17	35.5	42.9	39.8	39.100	40.410		36	36.1	49.9	40.7	40.178	41.227	
Upper jaw length	34.7	17	31.4	39.1	34.8	34.238	35.362		36	27.1	36.1	32.5	32.084	32.916	
	COUNTS														
Branched dorsal-fin rays	7	17	7	7	7.0			0.000	36	6	7	6.9			0.232
Branched pectoral-fin rays	7	17	7	9	7.9			0.458	36	7	8	7.8			0.378
Branched pelvic-fin rays	6	17	6	7	6.1			0.243	36	6	6	6.0			0.000
Branched anal-fin rays	13	17	12	14	12.9			0.556	36	12	14	12.9			0.439
Horizontal scale rows between dorsal- and anal-fin origins	8	17	8	8	8.0			0.000	–	–	–	–			–
Predorsal scales	15	15	14	15	14.9			0.258	–	–	–	–			–
Perforated lateral-line scales	3	8	3	6	4.9			0.991	–	–	–	–			–
Lateral series scales	32	14	32	35	33.9			0.770	–	–	–	–			–
Horizontal scale rows around caudal peduncle	13	17	13	13	13.0			0.000	–	–	–	–			–
Dorsal limb gill rakers	5	17	5	6	5.3			0.470	–	–	–	–			–
Ventral limb gill rakers	10	17	9	10	9.6			0.493	–	–	–	–			–
Vertebrae	34	17	33	35	34.4			0.608	43	34	36	35.3			0.492

---

[1] Rio Bodoquena, Brazil, MNRJ 4124 (holotype), MNRJ 4125, CAS (SU) 40764.

[2] Arroyo Curimbaty, Paraguay, UMMZ 205414.

[3] Arcsine transformations were used for calculating the 95% confidence limits.

TABLE 2.—Morphometrics and meristics of *Xenurobrycon macropus*.

Character	Paraguay, Lago Ypacarai[1]				Paraguay, Río Corrientes[2]						
		Range				Range			95% Confidence limits[3]		
	n	low	high	x̄	n	low	high	x̄	L_1	L_2	SD
Standard length (mm)	4	14.4	17.1	15.5	12	13.9	17.9	16.0			1.226
					PERCENTAGE OF STANDARD LENGTH						
Greatest body depth	4	26.3	31.2	29.4	11	24.3	28.8	27.0	26.381	27.619	
Depth at dorsal-fin origin	4	26.3	29.6	28.6	12	24.3	28.0	26.7	26.270	27.130	
Snout to dorsal-fin origin	4	61.8	64.3	62.7	12	59.8	63.4	61.4	61.053	61.747	
Snout to pectoral-fin origin	4	23.6	24.7	24.2	12	22.7	26.1	24.2	23.750	24.649	
Snout to pelvic-fin origin ♂	2	32.9	33.8	33.4	6	33.6	37.0	35.4	34.559	36.242	
Snout to pelvic-fin origin ♀	2	43.3	46.5	44.9	6	41.6	44.3	43.0	42.451	43.549	
Snout to anal-fin origin	4	62.5	63.9	63.0	12	58.1	63.4	60.8	60.163	61.437	
Caudal peduncle depth ♂	2	15.8	16.2	16.0	6	12.3	13.8	13.4	12.890	13.904	
Caudal peduncle depth ♀	2	11.7	12.5	12.1	6	11.0	11.8	11.5	11.229	11.771	
Caudal peduncle length	4	20.5	23.7	22.3	12	21.1	23.4	22.2	21.899	22.501	
Pectoral-fin length	4	20.8	23.4	21.6	11	20.2	23.0	22.0	21.577	22.423	
Pelvic-fin length ♂	2	39.6	40.8	40.2	6	35.1	40.9	37.5	36.115	38.885	
Pelvic-fin length ♀	2	12.9	13.2	13.1	6	12.7	14.5	13.3	12.736	13.864	
Dorsal-fin base length	4	7.0	8.6	7.9	12	7.8	9.3	8.4	8.070	8.730	
Longest dorsal-fin ray length	3	20.1	23.4	22.2	11	20.2	24.3	22.4	20.767	23.033	
Anal-fin base length	4	18.2	20.1	19.0	12	19.0	22.1	20.5	20.044	20.956	
Anal-fin lobe length ♂	2	28.9	29.9	29.4	6	20.1	24.5	22.8	21.737	23.863	
Anal-fin lobe length ♀	2	17.5	18.8	18.2	6	15.6	19.2	18.2	17.141	19.259	
Bony head length	4	21.5	22.4	21.9	12	21.5	25.0	23.5	23.015	23.985	
					PERCENTAGE OF BONY HEAD LENGTH						
Horizontal eye diameter	4	43.2	45.2	44.2	12	39.0	46.2	42.8	41.971	43.629	
Snout length	4	18.9	23.5	21.3	12	17.9	24.4	21.5	20.579	22.421	
Least width interorbital	4	41.2	46.0	44.1	12	35.8	41.7	38.7	38.006	39.394	
Upper jaw length	4	29.0	32.4	30.9	12	28.9	38.6	32.2	31.159	33.241	
						COUNTS					
Branched dorsal-fin rays	4	7	7	7.0	12	7	8	7.3			0.452
Branched pectoral-fin rays	4	7	7	7.0	12	6	8	7.8			0.622
Branched pelvic-fin rays	4	6	6	6.0	12	6	6	6.0			0.000
Branched anal-fin rays	4	12	13	12.5	12	13	14	13.2			0.389
Horizontal scale rows between dorsal- and anal-fin origins	4	8	8	8.0	4	8	8	8.0			0.000
Predorsal scales	4	15	15	15.0	2	15	15	15.0			0.000
Perforated lateral-line scales	4	4	5	4.3	–	–	–	–			–
Lateral series scales	4	33	34	33.3	–	–	–	–			–
Horizontal scale rows around caudal peduncle	4	13	13	13.0	3	13	13	13.0			0.000
Dorsal limb gill rakers	4	5	6	5.3	–	–	–	–			–
Ventral limb gill rakers	4	8	9	8.3	–	–	–	–			–
Vertebrae	4	34	35	34.5	12	34	36	35.1			0.515

[1] Lago Ypacarai, Paraguay, USNM 219381, USNM 219382.

[2] Rio Correntes, Paraguay, UMMZ 205419.

[3] Arcsine transformations were used for calculating the 95% confidence levels.

Seventh through tenth rays of dorsal caudal-fin lobe modified in shape and position with strong interradialis muscles extending beyond their midlengths (Figure 47). Distal portion of these rays curved strongly ventrally and overlapping dorsal rays of ventral lobe. Membrane between lobes complete. In any given specimen all overlapping rays of dorsal lobe lie to one side of ventral lobe, either right or left (Figure 67). Note that in Figure 11 rays in middle of fin are drawn without overlap so that all rays may be seen clearly; actual extent of curvature in rays of both upper and lower lobes is greater than depicted. Tenth ray of dorsal lobe in specimen illustrated bears an angle at joint between third and fourth ray segments (counting basal segment); this joint abutting ninth ray dorsally (Figure 11, inset). Details of this arrangement vary somewhat from specimen to specimen, with a continuous curve rather than a sharp angle in some specimens. Dorsal ray of ventral caudal-fin lobe (= eleventh principal caudal-fin ray) forms interrupted sigmoid curve and is termed here sigmoid ray. Base of each sigmoid-ray half with large unciform dorsal process extending across hypural 2 and terminating lateral to hypural 3. Sigmoid-ray base movably articulated on distal border of hypural 2. Posterior to point of articulation with hypural 2, sigmoid ray enlarged and directed posterodorsally; ossification of ray interrupted for a distance approximately equivalent to two ray segments so that remainder of ray is detached from ray base. Remainder of ray curved ventrally. Ossification of two adjacent ventral-lobe rays also interrupted; ray segments, where ossified, very narrow. Base of seventeenth principal ray expanded laterally into projecting lobe, base of sixteenth ray expanded laterally but not lobed.

Eighteenth principal caudal-fin ray bears thin, flat bilateral projections with rounded distal borders; each projection formed of fourth and fifth ray segments, ventrolaterally expanded and often fused in their expanded portions (Figures 11, 47). Ventral to shelf, between bilateral projections, ray surface is concave rather than convex. These lamellae situated slightly ventral to pouch scale at point where border of scale flares slightly laterally. Flaring border marks ventral opening to a space medial to large scale.

All principal caudal-fin rays of males dorsoventrally expanded along their distal portions. Ventral principal ray (unbranched) with especially large expansion along distal two-thirds of its ventral margin. Two adjacent procurrent rays also with ventral expansion on their distal portions.

Procurrent caudal rays relatively few. Number of ventral procurrent rays in cleared and stained specimens 6 in both male and female; number of dorsal procurrent rays 6 in female and 5 in male.

Structure of hypurals sexually dimorphic. Hypural skeleton of females exhibits typical characid morphology. In sexually mature males, hypural 1 fused to parhypural. Hypural 2 does not extend as far posteriorly as other hypurals; distal margin of hypural 2 lacks cartilage. Posterior margin of hypural skeleton angled slightly anteroventrally rather than being approximately perpendicular to longitudinal axis of fish, with hypural 6 extending further posteriorly than parhypural-hypural 1 element. Since principal fin rays articulate along this diagonal border, entire caudal fin shows a ventral tilt as noted in original description, Myers and P. de Miranda-Ribeiro (1945:4). Development of flanges on neural and haemal spines in caudal area greater in males than in females.

Caudal squamation sexually dimorphic. Females and sexually immature specimens with large, approximately circular scale extending from ventral portion of dorsal lobe to ventral branched ray of ventral lobe; radii along posterior margin of this scale numerous but not as numerous or closely spaced as in male. Other caudal scales of females and sexually immature specimens similar to precaudal scales but with more radii along posterior margin. This large scale becomes modified in maturing males (Figure 31) and eventually becomes the pouch scale of mature males.

Caudal squamation of sexually mature males with pouch scale located near middle of caudal-fin base, approximately round, with short, blunt protuberance posteriorly (Figures 11, 25, 28). Accessory pouch scale slightly enlarged; this scale bears more radii than other scales surrounding largest scale and is only lightly ossified in area of radii. Radii on pouch scale present along posterodorsal and posteroventral scale borders; middle area of scale and distal border of posterior process usually without radii. Radii numerous and closely spaced, particularly along posteroventral border (Figure 28). Ventral margin of pouch scale well ossified but connective tissue of radial striae allows considerable lateral expansion of scale margin in alcohol specimens. Pouch scale well ossified along curved anterior margin and with pronounced ridge on medial surface; this ridge set in from border of scale. Anterior region of pouch scale shallowly arched laterally over mass of modified muscle tissue (p. 97). Posterior portion of pouch scale surface relatively flat, with posterodorsal border curved slightly medially and posteroventral border flared slightly laterally. Posterior apex of pouch scale tightly bound by connective tissue at its border to principal ray 10 and by two more or less distinct ligaments from the medial surface of pouch scale to immediately adjacent parts of rays 10 and 11. Posterodorsal portion of pouch scale bound by connective tissue to underlying muscle tissue. Posteroventral margin and middle area of pouch scale free from underlying tissue, easily lifted slightly laterally without breaking skin or connective tissue. However, only a small sac-like area present, no large caudal pouch as in *Corynopoma riisei* (Atkins and Fink, 1979:466).

Modified epidermal tissue, presumably glandular, occurs on male caudal fin. Description of this tissue in region of presumed caudal gland limited to gross morphology evident on alcohol specimens using a Leitz Widefield dissecting microscope. Two patches of modified epidermis consistently distinguished on sexually mature males. Most obvious is a pad of thick white tissue on fin-ray surface in area of posteroventral radii of pouch scale. This occurs both medial to pouch scale and posteroventral to pouch scale border. This tissue associated with a thin flap of skin extending dorsally from principal ray 17 to approximately ray 15. Pad of tissue not extending onto dorsal surface of ventrolateral shelflike process of ray 18 and a groove occurs in tissue between pad and shelflike process. Second area of whitish tissue on interradial membrane under middle region of pouch scale less obvious. This tissue occurs on fleshy protuberance in hiatus between sigmoid ray (ray with unciform process) and other rays of ventral lobe. Thick tissue extends over proximal portion of ventral lobe posteroventral to pouch scale in some specimens. This may also be modified glandular tissue (see whitish area on ventral portion of ventral caudal-fin lobe, Figure 67). Thick tissue associated with proximal part of four sharply decurved rays of dorsal caudal-fin lobe formed of muscle, not glandular tissue as originally described by Myers and P. de Miranda-Ribeiro (1945:4).

Caudal-fin musculature sexually dimorphic. Caudal-fin musculature of male modified (Figures 47, 67); compare with female (Figure 3). Separate posteromedian sections of hypaxialis and epaxialis muscle groups thick; hypaxialis section especially large, extending distinctly dorsal to lateral midline. Epaxialis section inserts by tendons onto principal caudal-fin rays 1 to 3. Hypaxialis section inserts by a tendon onto eighteenth ray. Some fibers of lateralis superficialis bundle extend across lateral midline, originating ventral to midline from myocommatum of ventral lateralis superficialis bundle and inserting tendinously to dorsal principal caudal-fin ray. Remaining fibers of ventral lateralis superficialis bundle insert by a tendon to eighteenth principal caudal-fin ray, separate from tendon of posteromedian hypaxialis section.

Major interradialis muscle mass divided into three separate bundles. One bundle attaches only to ventral caudal-lobe fin rays, originating just distal to bases of fin rays 12 to 17 and inserting on lateral face of sigmoid ray (ray 11) ("interradialis-a," Figure 47). (We reverse usual origin and insertion of this muscle in this description because this muscle, when contracted, probably moves sigmoid ray on its hypural 2). Another muscle mass ("interradialis-b," Figure 47), originates along posterior margin of unciform process and ray base of sigmoid ray and inserts on medial face of largest caudal scale. Site of insertion forms a nearly continuous semicircle near margin of large scale; fibers attach most densely at area of curved posterodorsal radii and in area of ventral radii (Figures 11, 28, 47). Third bundle consists of fibers of dorsal lobe caudal-fin rays; fibers insert along distal, decurved portions of rays 7 to 10.

Caudal-fin musculature of female much thinner than that of male. Posteromedian section of hypaxialis does not extend dorsal to lateral midline. Fibers of lateralis superficialis do not cross midline; posterior fibers of ventral bundle are all directed posteroventrally. Large interradialis muscle sheet with no separate bundles, similar to that of most other characids. Attachments of posteromedian epaxialis and hypaxialis sections and of lateralis superficialis bundles very difficult to ascertain, but appear to be like those of male.

Scales cycloid with few radii along posterior margins except scales along narrow dorsal and ventral body surfaces and in caudal region. Scales often absent, apparently rubbed off by other fishes in preservative during transport after collecting (Tables 1, 2). Lateral line incomplete. Perforated lateral-line scales 3 to 6. Scale rows between dorsal-fin origin and anal-fin origin 8 in all specimens. Scale rows around caudal peduncle 13 in all specimens; a median row is absent on ventral surface of caudal peduncle at it narrowest point. Predorsal scales 14 to 15, usually 15.

Teeth of all jaw bones conical (Figures 63, 64*a*). Teeth, especially smaller, posterior teeth, often buried in tissue, making accurate counts nearly impossible, but type series with this tissue nearly gone, making accurate counts possible. Premaxillary teeth almost in a single uneven row, but usually with a few teeth clustered anteromedially; holotype 7; paratypes n = 15, range = 7 to 10, $\bar{x}$ = 7.9, SD = 0.961. Some specimens from Sete Quedas, Brazil, MZUSP 13966-69 and Lago Ypacarai, Paraguay, USNM 219382, with as few as 6 premaxillary teeth. Maxillary teeth in a single even row but with anterior teeth projecting somewhat anteriorly; holotype 4; paratypes n = 15, range 4 to 7, $\bar{x}$ = 5.1, SD = 0.915. One specimen from tributary of Arroyo Curuguaty, Paraguay, UMMZ 206314, with 8 maxillary teeth. Dentary teeth in a single row, always with medial tooth angled slightly inward and adjacent tooth projecting outward; holotype 10; paratypes n = 15, range 11 to 14, $\bar{x}$ = 11.1, SD = 1.125. One male from Sete Quedas, Brazil, MZUSP 13966–69, with 8 dentary teeth.

See Tables 1, 2 for vertebral counts including Weberian apparatus and terminal compound centrum and for gill-raker counts. Branchiostegal rays in two cleared and stained specimens, 4, all originating from anterior ceratohyal.

COLOR IN ALCOHOL.—Description of male and female specimens from Lago Ypacarai, Paraguay (Figure 3), with comments on specimens from other localities as appropriate. Entire body pale brown, nearly white, probably silvery in life but guanine pigment lost due to initial preservation in formalin. Dark brown narrow midside stripe extends from near dorsal part of opercular opening to caudal-fin base. Stripe may or may not be well developed anteriorly (compare male and female, Figure 3). Scattered dark brown chromatophores occur close to lateral stripe. Chromatophores may be nearly absent anteriorly. Caudal peduncle always with dark brown chromatophores at base of dorsal lobe of caudal fin. These chromatophores may be scattered or relatively dense. In male, this chromatophore cluster extends slightly ventral to midline stripe but does not extend onto anterior border of large caudal-fin scale, thus forming a crescent. A few scattered dark brown chromatophores present in area of large caudal scale. Area dorsal to lateral midside stripe with scattered dark brown chromatophores arranged along scale borders. These in life may give upper half of body a reticulate pattern (Figure 3, female). Some male specimens show almost no dark chromatophores in this area except on scale borders along dorsum (Figure 3, male). Area ventral to horizontal midside stripe usually with chromatophores only in area dorsal to anal-fin base and along ventral border of caudal peduncle. In male, area of large muscle mass serving pelvic fin with scattered dark brown chromatophores.

Scattered chromatophores occur on dorsal, anal, and caudal fins. Pectoral fins of males hyaline except for dark brown chromatophores along anterior rays. Pelvic fins of males with dark brown chromatophores along rays; chromatophores more dense along anterior rays. Pectoral and pelvic fins of females nearly hyaline.

Opercle, cheek (area of orbital bones), and lower jaw with very few dark chromatophores. Dorsum of head in supraoccipital, parietal, and posterior frontal regions appearing nearly black from presence of numerous very dark brown chromatophores. Head dorsal to eye, in area of anterior part of frontal bones, dark with fairly dense dark chromatophores. Nasal area and tip of snout also dark brown.

SEXUAL DIMORPHISM.—Tables 1 and 2 present morphometric data for specimens of *Xenurobrycon macropus* arranged by sex for four characters out of 31. All populations show some obvious sexual differences in distance from snout to pelvic-fin origin, depth of caudal peduncle, length of pelvic fin, and length of anterior lobe of anal fin. Anterior placement of pelvic girdle and increased length of pelvic fin in males account for most of marked morphometric differences. Hooks present on pelvic, anal, and caudal fins of males; females lack hooks.

Analysis of covariance using logarithmic transformed data for 21 morphometric characters by sex were done for two population samples, the type series, MNRJ 4124, MNRJ 4125, and CAS(SU) 40764, all from Rio Bodoquena, Brazil, and UMMZ 205414 from Arroyo Curimbaty, Paraguay. These samples are relatively small, mostly of adults, and often the coefficients of determination (correlation) for regression were low, indicating lack of regression. This was especially true for the males for which there was little variation in size of the adult samples and which appear to be subject to sexual maturation at varying sizes within that restricted range. (For discussion of male maturation size, see p. 38). However, intercepts (rarely slopes) showed significant differences ($P<0.01$ determined in a two-tailed test) between males and females for the four characters listed above and compared in Tables 1, 2. No other characters showed significant differences in the type series, but such differences did occur in intercepts of anal-fin base length on standard length, longest dorsal-fin ray length on standard length (greater in the males for both), and in greatest body depth on standard length (greater in females) for specimens from Arroyo Curimbaty. The females were full of ripe eggs and therefore deeper in body than the males. The other two characters, longest dorsal-fin ray length and anal-fin base length, showed these differences in one population sample of *X. heterodon* (page 93). Complex glandular, muscular, and osteological structures present in caudal fin of males absent in females are described above (p. 77).

POPULATION VARIATION.—Sample size is too small for rigorous analysis of morphometric differences. Furthermore, the population samples differ in ways that make statistical comparisons for many measurements useless for a study of geographic variation. For example, all specimens in the type series from Rio Bodequena were preserved in alcohol and are now soft (but not shrunken) and do not provide measurements of the accuracy required. In addition, specimens in this population sample were in breeding condition, the females rotund with eggs. On the other hand, the samples from Paraguay, various UMMZ numbers, were preserved in formalin, are now somewhat shrunken, and were not in breeding condition when captured, except for UMMZ 205414. The UMMZ specimens also lack scales (presumably rubbed off by friction with larger fishes while in transit in preservatives), while the type series retain their scales. In small fishes such as these the presence and absence of scales affects the measurements and body proportions.

ETYMOLOGY.—The name *macropus* is from the Greek *makros* (long) and *pous* (foot), hence pelvic appendage; "long-foot" in reference to the elongate pelvic fin of the male.

Xenurobrycon pteropus, new species

FIGURES 4, 29, 43, 64*b*, 78

MATERIAL EXAMINED.—BRAZIL: MZUSP 12412, holotype, male, SL 13.5 mm, and USNM 232921, cleared and stained, paratype, male, SL 13.8 mm; Amazonas: an igarapé in Fonte Boa, approximately 2°30′S, 67°2′W, EPA, 25 Oct 1968.

DIAGNOSIS.—Premaxilla with wavy series of at least 6 to 7 conical teeth, some anterior teeth of series pointing anterolaterally; 2 exserted "tusk" teeth external to wavy series (Figure 64*b*). Maxilla with single row of 6 conical teeth. Anterior tooth exserted, forming a "tusk" tooth, second maxillary tooth pointing ventrolaterally but much less than exserted tooth, each of remaining maxillary teeth directed in succession less anteriorly and more ventrally than its anteromedial neighbor. Dentary with single row of 11 to 13 conical teeth. Adipose fin present. Adult males with following sexually dimorphic features: pouch scale shaped as illustrated in Figure 29, approximately rounded but with a short, relatively blunt protuberance posteriorly. Eighteenth principal caudal-fin ray (counting ventrally from dorsal principal caudal fin-ray) without platelike bilateral projections but with each ray half in this region bearing a narrow ventrolateral ridge, as in young, maturing males of *Xenurobrycon macropus*. Bony hooks on fourth through eleventh branched anal-fin rays, posterior four of these hooks larger than more anterior hooks.

DESCRIPTION.—See Table 3 for morphometrics and meristics. In all cases n = 2. Body moderately elongate, sides compressed. Greatest body depth about midway between nape and dorsal-fin origin or closer to dorsal-fin origin. Predorsal body profile gently convex to tip of snout. Body profile slightly elevated at dorsal-fin origin, slightly concave along dorsal-fin base and nearly straight to origin of dorsal procurrent caudal-fin rays. Dorsal fin nearer to caudal-fin base (hypural joint) than to snout tip. Ventral body profile gently convex from anterior tip of lower jaw to pelvic-fin origin, somewhat concave in region of pelvic-fin insertion. Body profile between pelvic-fin insertion and anal-fin origin slightly convex in males, unknown for females. Profile gently concave along anal-fin base and nearly straight from posterior termination of anal-fin base to origin of ventral procurrent caudal-fin rays.

Head and snout moderately elongate. Lower jaw protruding slightly beyond upper jaw or jaws equal. Mouth angled anterodorsally from mandibular joint to snout tip. Maxilla terminating just anterior to a point on a vertical line drawn ventrally from anterior border of eye.

Dorsal-fin rays ii,7; last ray not split to its base. Adipose fin present. Anal-fin rays iii,13; last anal-fin ray split to its base. Anal fin with a strongly lobed anterior portion in holotype, less so in paratype, condition unknown in females. Anal fin of males (Figure 43) with bilateral antrorse to dorsally directed bony hooks; hooks beginning on third unbranched ray of holotype and on fourth branched ray of paratype and present on all posteriorly successive rays except terminal ray of holotype and terminal two rays of paratype. Usually one hook per segment, occasionally two, especially anteriorly. Anterior rays with largest number of hooks; hooks progressively fewer but larger posteriorly. Holotype with largest unbranched anterior ray bearing 6 hooks, first branched ray with 9, second with 7, third with 5, fourth with 4, fifth with 2, and all remaining hook-bearing rays with one hook except the tenth, which has two hooks. Posterior 4 or 5 hooks on eighth to twelfth rays much larger than anterior hooks.

Pectoral-fin rays i,8 in both specimens. Distal tips of pectoral-fin rays extend well posterior to pelvic-fin origin in males.

Pelvic-fin rays i,7. Pelvic fin presumably sexually dimorphic (females unknown), greatly elongate in males. Pelvic-fin origin much nearer pectoral-fin origin than anal-fin origin males. Pelvic

TABLE 3.—Morphometrics and meristics of *Xenurobrycon pteropus* and *Xenurobrycon heterodon*.

Character	*Xenurobrycon pteropus*[1]			*Xenurobrycon heterodon*[2]				
		Range				Range		
	n	low	high	Holotype	n	low	high	x̄
Standard length (mm)	2	13.5	13.8	16.2	7	16.2	17.2	16.7
				PERCENTAGE OF STANDARD LENGTH				
Greatest body depth	2	27.4	30.4	29.6	7	26.8	29.6	28.5
Depth at dorsal-fin origin	2	27.4	29.7	28.4	7	23.8	28.4	26.3
Snout to dorsal-fin origin	2	59.3	60.9	61.1	7	58.3	63.5	61.1
Snout to pectoral-fin origin	2	25.9	27.5	22.8	7	20.9	23.8	22.7
Snout to pelvic-fin origin ♂	2	34.8	36.2	33.0	4	31.9	33.3	32.5
Snout to pelvic-fin origin ♀	–	–	–	–	3	44.1	46.1	45.0
Snout to anal-fin origin	2	60.0	60.0	61.7	7	58.7	62.9	60.7
Caudal peduncle depth ♂	2	14.1	15.2	13.6	4	12.8	13.6	13.2
Caudal peduncle depth ♀	–	–	–	–	3	11.2	11.6	11.4
Caudal peduncle length	2	20.7	22.5	21.6	7	19.8	22.0	21.5
Pectoral-fin length	2	20.7	22.5	23.5	7	18.0	23.5	21.2
Pelvic-fin length ♂	2	36.3	37.0	37.7	4	35.5	37.8	36.7
Pelvic-fin length ♀	–	–	–	–	3	11.6	12.4	12.0
Dorsal-fin base length	2	9.6	10.1	9.3	7	7.6	9.3	8.2
Longest dorsal-fin ray length	2	21.5	23.2	23.5	7	20.4	23.8	22.5
Anal-fin base length	2	23.0	23.2	21.0	7	19.6	21.6	20.7
Anal-fin lobe length ♂	2	24.4	25.4	24.1	4	20.9	24.1	22.9
Anal-fin lobe length ♀	–	–	–	–	3	18.6	19.4	19.1
Bony head length	2	24.4	26.1	21.6	7	20.4	22.8	21.4
				PERCENTAGE OF BONY HEAD LENGTH				
Horizontal eye diameter	2	38.9	42.4	45.7	7	42.5	48.6	46.1
Snout length	2	21.2	22.2	22.9	7	20.0	22.9	21.6
Least width interorbital	2	36.1	39.4	42.9	7	38.9	44.1	41.7
Upper jaw length	2	30.6	33.3	31.4	7	27.0	33.3	30.8
				COUNTS				
Branched dorsal-fin rays	2	7	7	7	7	6	7	6.9
Branched pectoral-fin rays	2	8	8	8	7	7	9	7.9
Branched pelvic-fin rays	2	7	7	6	7	6	6	6.0
Branched anal-fin rays	2	13	13	14	7	13	14	13.7
Horizontal scale rows between dorsal- and anal-fin origins	2	8	8	8	7	8	8	8.0
Predorsal scales	2	13	13	15	7	15	16	15.3
Perforated lateral-line scales	2	3	4	6	4	4	6	5.0
Lateral series scales	2	32	32	35	4	33	35	34.3
Horizontal scale rows around caudal peduncle	2	13	13	13	7	13	13	13.0
Dorsal limb gill rakers	2	4	4	4	7	4	5	4.6
Ventral limb gill rakers	2	8	8	8	7	8	10	8.9
Vertebrae	2	34	34	34	7	34	36	34.7

[1] *Xenurobrycon pteropus*, igarapé in Fonte Boa, Brazil, MZUSP 12412 (holotype), USNM 232921 (paratype).

[2] *Xenurobrycon heterodon*, Río Bobonaza, Ecuador, KU 17925 (holotype), KU 17926, USNM 219389, USNM 219390.

fin of males arched and with interradial membranes as in *Xenurobrycon macropus*. Fins from an umbrella-like canopy when spread.

Pelvic fins of males with unpaired ventral bony hooks as in *X. macropus*. Hooks occur along nearly entire border of anterior ray and along more than half of second ray and medial two rays; rays in middle of fin with fewer hooks. Hooks occur on all branches of all rays. Paratype has one or more hooks per ray segment. Anterior ray of paratype with 28 hooks distributed over 18 ray segments, second ray with 26 hooks distributed over 14 segments, third ray with 22 hooks on 13 segments, fourth ray with 27 hooks on 11 segments, fifth ray with 29 on 15 segments, sixth ray with 33 on 19 segments, and seventh ray with 26 on 19 segments. All hooks are antrorse.

Pelvic girdle of males similar to that described above for male *Xenurobrycon macropus*.

Caudal fin with principal rays 10/9. Caudal-fin osteology of males similar to that of *X. heterodon*. Bony hooks are present on principal rays 1 to 3, 6 to 7, and 18 and 19 in holotype, paratype damaged. Caudal scale (Figure 29) intermediate in length, numbers of radii, and bluntness of posterior apex between those conditions present in scales of *X. macropus* and *X. heterodon* (Figures 28, 30).

Scales cycloid with few radii along posterior margins except for scales along narrow dorsal and ventral body surfaces and in caudal region. Lateral line incomplete. Perforated lateral-line scales 3 to 4. Lateral series scales to hypural joint 32 in both specimens. Scale rows between dorsal-fin origin and pelvic-fin origin 8 in both specimens. Scale rows around caudal peduncle 13 in both specimens. Predorsal scales 13 in both specimens.

Teeth of all jaw bones conical (Figure 64*b* of paratype). Premaxilla with a wavy series of 6 teeth in holotype, 7 in paratype; some of anterior teeth of this series angled anterolaterally. Dorsal to this series are 2 exserted "tusk" teeth. Maxillary teeth in an angled row of 6 conical teeth in both specimens, with anterior tooth an exserted "tusk" tooth, second tooth projecting slightly outward, and each of remaining teeth directed in succession less anteriorly and more ventrally than its anteromedial neighbor. Dentary with a row of 10 (holotype) to 12 (paratype) teeth, with anterior 6 to 8 angled somewhat outward. Ventral to anterior part of this row occurs one exserted "tusk" tooth in the paratype along with a replacement tooth for a second "tusk" tooth. This region cannot be seen clearly in the holotype without dissection.

See Table 3 for vertebral count including Weberian apparatus and terminal compound centrum and for gill raker count.

Branchiostegal rays 4, all originating from anterior ceratohyal.

COLOR IN ALCOHOL.—(Description of holotype, Figure 4). Entire body pale brown, nearly white, probably silvery in life. Dark brown midside stripe covers most of fourth horizontal scale row, counting ventrally from dorsal-fin origin. Stripe extends from near dorsal part of opercular opening to caudal-fin base. Caudal peduncle in both specimens with dark brown chromatophores at base of dorsal lobe of caudal fin. Area dorsal to lateral midside stripe with dark brown chromatophores distributed along scale borders, giving upper half of a body a reticulate pattern. Area ventral to horizontal midside stripe usually with chromatophores only in area dorsal to anal-fin base, area of vent, and along ventral border of caudal peduncle. Remainder of body with only a few scattered dark chromatophores.

Scattered chromatophores occur on dorsal, anal, pelvic, pectoral, and caudal fins. These chromatophores often organized along borders of fin rays. Otherwise fins nearly hyaline.

Opercle and cheek (area of orbital bones) with very few dark chromatophores; a few dark chromatophores present along vertical border between opercle and preopercle. Lower jaw with scattered dark chromatophores just ventral to tooth bases and a few scattered along the mandibular ramus. Dorsum of head in supraoccipital, parietal, and posterior frontal regions appearing nearly black from presence of numerous very dark brown chromatophores. Head dorsal to eye in region of anterior part of frontal bones, dark with fairly dense dark chromatophores. Upper jaw and snout with dark chromatophores, but area around nares relatively free of chromatophores.

ETYMOLOGY.—The name *pteropus* is from the Greek *pteron* (feather or wing) and *pous* (foot), hence pelvic appendage; "wing-foot" in reference to the large wing-shaped pelvic fins.

Xenurobrycon heterodon, new species

FIGURES 5, 12, 30, 34*e*, 55, 65

MATERIAL EXAMINED.—ECUADOR: KU 17925, holotype, male, SL 16.2 mm; KU 17926, paratypes, 1 male, 1 female, SL 16.3–17.2 mm; USNM 219389, paratypes, 1 male, 1 female, SL both 17.0 mm; USNM 219390, paratypes, 1 male, 1 female, SL 16.4–16.7 mm; Pastaza: Río Bobonaza at Sarayacu, 1°16′S, 78°31′W, G.R. Smith and J.D. Lynch, 12–22 Jul 1968. FMNH 94940, paratypes, 12 adults, SL 17.5–18.5 mm; MEPN (uncatalogued), paratypes, adults, SL 16.8–18.2 mm; Napo: Río Aguarico, tributary of Río Napo, 0°5′S, 76°31′W, D. Stewart, M. Ibarra, and R. Barriga, 20 Oct 1983.

PERU: USNM 219391, paratypes, 12 (including 2 cleared and stained) juveniles to adults, SL 13.8–16.7 mm; FMNH 87544, paratypes, 12 juveniles to adults, SL 14.1–16.4 mm; MCZ 54255, paratypes, 12 juveniles to adults, SL 13.9–16.2 mm; Huanuco: Río Pachitea, across river from Hotel Puerto Inca in Puerto Inca, 9°19′S, 75°4′W, D. and T. Greenfield and G. Glodek, 29 Jul 1975.

DIAGNOSIS.—Premaxilla (Figure 65) with 6 to 11 ($\bar{x} = 8.5$) teeth, some exserted anteriorly from others to varying degrees, including 1 or 2 exserted "tusk" teeth. Teeth not in well-defined rows. Premaxilla with medial "cluster" of 3 or 4 teeth of which 1 or 2 are offset anteriorly. This accompanied by a more laterally situated oblique row of 6 to 8 teeth of which medial 1 or 2 are tusk teeth. Exserted teeth conical; nonexserted teeth usually conical but sometimes with 1 or 2 small supplemental cusps. Maxilla with single row of 5 to 7 ($\bar{x} = 5.5$) conical teeth, anterior 1 or 2 of these exserted, forming "tusk" teeth. Dentary with single row of 9 to 12 ($\bar{x} = 10.4$) teeth; anterior 3 or 4 often with 3, sometimes 4, cusps. Adipose fin absent. Adult males with following features: pouch scale approximately teardrop shaped (Figures 12, 30). Eighteenth principal caudal-fin ray (counting ventrally from dorsal principal caudal-fin ray) without platelike bilateral projections but with each ray half in this region bearing a narrow ventrolateral ridge as in young, maturing males of *X. macropus* (figure 11; (compare with Figure 12). Bony hooks sometimes present on large unbranched and 9 or 10 anterior branched anal-fin rays, their presence probably seasonal and associated with breeding. (See Fink and Weitzman, 1974:22), and p. 89 regarding seasonality in characid fin hooks).

DESCRIPTION.—See Tables 3 and 4 for morphometrics and meristics. Measurements are given separately for males and females for four characters. Body moderately elongate, sides compressed. Greatest depth about midway between nape and dorsal-fin origin or sometimes at dorsal-fin origin. Predorsal body profile gently convex to tip of snout. Body profile slightly elevated at dorsal-fin origin, slightly concave along dorsal-fin base and nearly straight to origin of dorsal procurrent caudal-fin rays. Dorsal-fin origin nearer to caudal-fin base than to snout tip. Ventral body profile gently convex from anterior tip of lower jaw to pelvic-fin origin, somewhat concave in region of pelvic-fin insertion. Body profile between pelvic-fin insertion and anal-fin origin slightly convex in males, slightly concave in females. Profile gently concave at base of anal fin and nearly straight from posterior termination of anal fin to origin of ventral procurrent caudal-fin rays.

Head and snout moderately elongate. Lower jaw protruding slightly beyond upper jaw or jaws equal. Mouth angled anterodorsally from mandibular joint to tip of snout. Maxillary bone extending posteriorly approximately to a point on a vertical line drawn ventrally from anterior border of eye.

Dorsal-fin rays ii,7 in nearly all specimens, ii,6 in one specimen from Río Bobonaza, Ecuador, and in one specimen from Río Aguarico, Ecuador. Last dorsal-fin ray not split to its base. Adipose fin absent. Anal-fin rays iii,13 to iii,14, usually iii,14; branched rays distributed as in Tables 3 and 4. Last anal-fin ray split to its base. Anal fin with a strongly lobed anterior portion in males, much less lobed in females. Anal fin of male from Río Bobonaza, Ecuador, with bilateral antrorse bony hooks on largest anterior unbranched ray and 9 to 10 anterior branched rays; total number of rays with hooks 11 in 3 males and 10 in 1 male. Males from Río Aguarico, Ecuador, similar to those from Río Bobonaza. Males from Río Pachitea, Peru, without hooks on anal fin but with bilateral small, irregularly surfaced eminences, apparently remnants of hooks, distributed as are hooks on Ecuadoran specimens.

Pectortal-fin rays i,8 in holotype; range i,7 to i,9 for all specimens, usually 8 branched rays. Distal tips of pectoral-fin rays extending posteriorly to pelvic-fin origin in females and well beyond that point in males due to anterior placement of pelvic fin in males.

Pelvic-fin rays i,6 in all specimens. Pelvic fin sexually dimorphic, greatly elongate in males. Male pelvic-fin origin much nearer pectoral-fin origin than anal-fin origin. Female pelvic-fin origin about equidistant between pectoral-fin origin and anal-fin origin. Compare snout to pelvic-fin origin ratios in Tables 3 and 4. Female pelvic-fin rays not elongate, without hooks, much like pelvic-fin rays of most female glandulocaudine characids. Pelvic fin of males arched with interradial membranes broad as described for *X. macropus*. As in *X. macropus*, fins form inverted boat-shaped canopy when spread with forceps. Males from Río Bobonaza and Río Aguarico, Ecuador, with bony hooks like those of *X. macropus*; males from Río Pachitea, Peru, without hooks but cleared and stained specimen with irregular eminences and rough spots, apparently hook remnants, which are especially obvious distally. (The hypothesis that hooks on these fishes are seasonal and were recently either shed or, less likely, resorbed in Peruvian specimens is corroborated by the presence of an unattached but well-developed hook caught in membrane of left pelvic fin of a cleared and stained specimen, 16.7 mm SL). Pelvic-fin rays of cleared and stained male 16.4 mm SL from Río Bobonaza, Ecuador, with mostly antrorse pelvic-fin hooks as follows: anterior large unbranched ray with 31 hooks distributed over 17 ray segments, with about 9 hooks on long basal ray segment and more distal segments with 1 to 3 hooks each. Second ray, branched, bears 43 hooks distributed over 21 segments of unbranched and branched portions of ray. Third ray bears 45 hooks distributed over 21 segments of branched and unbranched portions of ray. Fourth ray bears 37 hooks over 18 segments of branched and unbranched portions of ray. Fifth ray, unbranched, bears 21 hooks distributed on 10 segments. Sixth ray, unbranched, bears 34 hooks on 17 segments, and seventh ray, unbranched, bears 33 hooks on 16 segments.

Pelvic girdles of males and females similar to girdles of *X. macropus*, except that in cleared and stained male from Río Pachitea, Peru, posteromedian processes are separated from each other by only about 0.7 mm or a distance just over ¼ length of pelvic girdle instead of 1.2 mm or a distance of more than ⅓ length of pelvic bone as in *X. macropus*.

Caudal fin with principal rays 10/9 in all specimens; caudal fin of females as in most other characids. Male caudal fin (Figure 12) similar to that described for *X. macropus* (Figures 11, 25, 47). Hooks very reduced to absent in males from Río Pachitea, Peru, but apparent hook remnants appear similar in distribution to hooks on male specimens from Río Bobonaza, Ecuador. Rays of dorsal and ventral caudal-fin lobes modified as in *X. macropus*, except that ventral branched ray lacks ventrolaterally projecting, bilateral laminae of bone. Concavity on ventral surface of this ray is present. Consequently, this ray with sharp ventrolateral borders in position of bilateral lamelle.

TABLE 4.—Morphometrics and meristics of *Xenurobrycon heterodon*.

Character	Ecuador, Río Aguarico[1]						
		Range			95% Confidence limits[3]		
	n	low	high	$\bar{x}$	L_1	L_2	SD
Standard length (mm)	24	16.3	18.5	17.4			0.584
	PERCENTAGE OF STANDARD LENGTH						
Greatest body depth	24	25.6	31.6	27.9	27.487	28.313	
Depth at dorsal-fin origin	24	22.7	27.6	24.4	24.079	24.721	
Snout to dorsal-fin origin	24	56.6	63.2	61.5	61.160	61.840	
Snout to pectoral-fin origin	24	20.1	24.1	21.8	21.536	22.064	
Snout to pelvic-fin origin ♂	7	31.4	32.7	32.2	31.895	32.505	
Snout to pelvic-fin origin ♀	17	41.8	46.0	44.3	44.090	44.710	
Snout to anal-fin origin	24	59.1	62.1	60.6	60.380	60.820	
Caudal peduncle depth ♂	7	12.3	13.7	12.8	12.425	13.175	
Caudal peduncle depth ♀	17	10.5	11.7	11.1	10.954	11.246	
Caudal peduncle length	24	19.6	22.8	21.2	20.968	21.432	
Pectoral-fin length	24	17.4	21.8	19.5	19.148	19.852	
Pelvic-fin length ♂	7	31.9	39.2	36.8	35.389	38.211	
Pelvic-fin length ♀	17	10.7	13.2	11.9	11.529	12.271	
Dorsal-fin base length	24	7.0	9.2	8.0	7.728	8.272	
Longest dorsal-fin ray length	23	19.3	22.3	21.0	20.757	21.243	
Anal-fin base length	24	19.3	22.4	20.5	20.260	20.740	
Anal-fin lobe length ♂	7	21.3	24.6	22.8	22.160	23.440	
Anal-fin lobe length ♀	16	16.7	18.9	17.8	17.517	18.083	
Bony head length	24	19.0	22.7	20.9	20.574	21.226	
	PERCENTAGE OF BONY HEAD LENGTH						
Horizontal eye diameter	24	37.0	47.1	43.1	42.564	43.635	
Snout length	24	17.6	22.3	19.8	19.498	20.102	
Least width interorbital	24	41.0	51.6	46.1	45.510	46.689	
Upper jaw length	24	31.3	39.2	34.8	34.275	35.325	
	COUNTS						
Branched dorsal-fin rays	24	6	7	7.0			0.204
Branched pectoral-fin rays	24	8	9	8.0			0.204
Branched pelvic-fin rays	24	6	6	6.0			0.000
Branched anal-fin rays	24	13	15	13.8			0.532
Horizontal scale rows between dorsal- and anal-fin origins	24	8	8	8.0			0.000
Predorsal scales	16	15	17	16.0			0.365
Perforated lateral-line scales	7	4	5	4.6			0.535
Lateral series scales	10	33	35	34.0			0.667
Horizontal scale rows around caudal peduncle	24	13	13	13.0			0.000
Dorsal limb gill rakers	24	4	5	4.9			0.338
Ventral limb gill rakers	24	9	12	10.0			0.590
Vertebrae	24	34	36	35.0			0.550

[1] Río Aguarico, Ecuador, FMNH 94940, MEPN (uncataloged).

[2] Río Pachitea, Peru, USNM 219391, FMNH 87544, MCZ 54255.

[3] Arcsine transformations were used for calculating the 95% confidence limits.

TABLE 4.—Continued.

Character	Peru, Río Pachitea[2]						
		Range			95% Confidence limits[3]		
	n	low	high	$\bar{x}$	L_1	L_2	SD
Standard length (mm)	14	13.6	16.7	15.0			1.031
	PERCENTAGE OF STANDARD LENGTH						
Greatest body depth	14	22.9	26.4	24.5	24.066	24.934	
Depth at dorsal-fin origin	14	22.1	25.3	23.0	22.621	23.379	
Snout to dorsal-fin origin	14	58.2	62.8	60.2	59.717	60.683	
Snout to pectoral-fin origin	14	23.4	25.4	24.1	23.886	24.314	
Snout to pelvic-fin origin ♂	4	33.3	34.0	33.6	33.312	33.888	
Snout to pelvic-fin origin ♀	10	42.7	44.9	43.4	43.128	43.672	
Snout to anal-fin origin	14	57.6	61.8	59.4	58.883	59.917	
Caudal peduncle depth ♂	4	12.0	13.4	12.8	11.990	13.610	
Caudal peduncle depth ♀	10	11.1	12.1	11.7	11.510	11.890	
Caudal peduncle length	14	20.6	23.8	22.2	21.845	22.555	
Pectoral-fin length	14	18.4	22.2	20.1	19.654	20.546	
Pelvic-fin length ♂	4	35.8	36.6	36.0	35.634	36.366	
Pelvic-fin length ♀	10	11.8	13.2	12.3	12.016	12.584	
Dorsal-fin base length	14	8.3	9.9	8.9	8.616	9.184	
Longest dorsal-fin ray length	14	20.1	24.4	22.1	21.655	22.545	
Anal-fin base length	14	18.9	23.1	21.1	20.594	21.606	
Anal-fin lobe length ♂	4	22.8	23.8	23.4	22.931	23.869	
Anal-fin lobe length ♀	10	18.2	20.4	19.1	18.807	19.393	
Bony head length	14	21.2	23.5	22.0	21.735	22.264	
	PERCENTAGE OF BONY HEAD LENGTH						
Horizontal eye diameter	14	41.9	46.9	43.8	43.234	44.366	
Snout length	14	19.4	22.9	21.7	21.239	22.161	
Least width interorbital	14	37.5	43.8	41.4	40.818	41.982	
Upper jaw length	14	30.3	34.4	32.6	32.085	33.114	
	COUNTS						
Branched dorsal-fin rays	15	7	7	7.0			0.000
Branched pectoral-fin rays	15	7	9	8.2			0.775
Branched pelvic-fin rays	15	6	6	6.0			0.000
Branched anal-fin rays	15	13	14	13.3			0.488
Horizontal scale rows between dorsal- and anal-fin origins	1	8	8	–			–
Predorsal scales	5	15	16	15.2			0.447
Perforated lateral-line scales	1	4	4	–			–
Lateral series scales	–	–	–	–			–
Horizontal scales rows around caudal peduncle	15	14	13	13.0			0.000
Dorsal limb gill rakers	12	4	5	4.8			0.452
Ventral limb gill rakers	12	8	9	8.8			0.452
Vertebrae	15	34	36	34.3			0.617

(Compare Figures 12 of *X. heterodon* and Figure 11 of *X. macropus.*)

Hypural skeleton of both males and females as in *X. macropus.*

Caudal squamation of female as in *X. macropus.* Caudal squamation of male as in *X. macropus,* except for certain chracteristics of pouch scale. Pouch scale approximately teardrop-shaped; its posterior field pointed with only a small portion of its distal border free of striated radii (Figure 30).

Morphology of presumed caudal gland of male as in *X. macropus,* except that no groove occurs in tissue of eighteenth principal caudal-fin ray. Caudal musculature of male as in *X. macropus* except that muscle bundles are less robust. Caudal musculature of female as in *X. macropus.*

The hypothesis proposed below for *X. macropus* regarding the functioning of a caudal "pump" applies to *X. heterodon* as well. Presumably the flattened margins of the eighteenth principal caudal-fin ray of *X. heterodon* do not deflect the pheromone-bearing water in the same manner as the bilateral platelike lamellae of *X. macropus.*

Scales cycloid with very few radii along posterior margins except in caudal region and along narrow dorsal and ventral body surfaces. Lateral line incomplete. Scales mostly missing in specimens from Río Pachitea, Peru; one male specimen with 4 perforated lateral-line scales and 32 scales in lateral series, excluding large caudal scale. Scale counts could be made on two specimens of each sex from Río Bobonaza, Ecuador. Holotype with 6 perforated lateral-line scales and 35 scales in lateral series including large caudal-fin scale. Usually about 34 lateral series scales. (See Tables 3 and 4 for distribution of perforated lateral-line and lateral series scale counts). Scale rows between dorsal-fin origin and pelvic-fin origin 8 in all specimens. This count could be made in only one specimen from Río Pachitea, but counts of pockets could be made. Scale rows around caudal peduncle 13 in all specimens. These scales missing in specimens from Río Pachitea, but counts of pockets could be made. As in other species of *Xenurobrycon,* a median ventral scale row is absent at the narrowest region of the caudal peduncle. Predorsal scales 15 in holotype; 14 to 16, usually 15 in other specimens (Tables 3, 4).

Teeth of jaws unicuspid, bicuspid, or tricuspid depending on position in jaws (Figure 65 and description below). Maxillary and dentary teeth in single row. Premaxilla with some teeth offset anteriorly to varying degrees, including 1 or 2 exserted "tusk" teeth; the resulting configuration not accurately described as either 1 row or 2 rows as those terms are usually applied in characid morphology. Teeth of holotype (values not in parentheses) as follows: Teeth of premaxilla and maxilla conical. Premaxilla with second and fourth tooth from midline offset anteriorly and projecting slightly anteriorly. Two (2 or 3) "tusk" teeth exserted from oral cavity (Figure 65) and with their bases dorsal to fourth tooth from midline. Lateral to 2 (2 to 3) "tusk" teeth are 5 (5 to 8, usually 5 or 6 in other specimens) additional teeth along lateral ramus of premaxilla, each of which in succession is directed less anteriorly and more ventrally than its anteromedial neighbor. Together with "tusk" teeth these form an oblique row across lateral portion of premaxilla. Maxilla with 7 (5 to 7, usually 5 or 6) teeth also forming a sharply angled row; anterior 2 teeth exserted and each of remaining 5 teeth directed, in succession, less anteriorly and more ventrally than its anteromedial neighbor. Dentary with 11 (9 to 12, usually about 10) teeth; medial 4 of these tricuspid and much larger than remaining 5 to 8. Smaller, lateral 5 to 8 teeth unicuspid and decreasing in size in an anterior to posterior sequence.

Premaxillary tooth counts in specimens from all localities, $n = 20$, range = 6 to 11, $\bar{x} = 8.5$, SD = 1.890. Premaxilla with 3 or 4 teeth "clustered" on its medial portion, usually with 3 (as in holotype). Remaining premaxillary teeth forming transverse row on lateral portion of premaxilla; usually 2 (occasionally only 1) of these teeth exserted. Premaxilla sometimes with multicuspid teeth: two males from Río Bobonaza with medial premaxillary tooth biscuspid, one female with 2 medial premaxillary teeth bicuspid, one female with 3 medial premaxillary teeth tricuspid, and cleared and stained female with left side having 5 of 6 nonexserted teeth bicuspid and right side having medial tooth bicuspid and laterally adjacent tooth tricuspid. Maxillary tooth counts as follows: n = 26, range = 5 to 7, $\bar{x}$ = 5.5, and SD = 0.982. All maxillary teeth unicuspid in all specimens, forming an angled row, with 2 exserted "tusk" teeth anteriorly. Dentary tooth counts as follows, n = 32, range = 9 to 12, $\bar{x}$ = 10.4, SD = 0.982. Dentary usually with medial 4 teeth (3 teeth in some) tricuspid, larger than remaining teeth. Some males and females with 5 tricuspid dentary teeth, with one of smaller teeth also being tricuspid.

Statistical comparison by use of two-tailed Student's t test using square-root transformations of numbers of teeth on each jaw bone for two population samples, one from Río Aguarico, the the other from Río Bobonaza (both in Ecuador), of *X. heterodon* showed no significant differences at the 0.05 level. Patterns of tooth arrangement in specimens from Río Aguarico almost the same as in specimens from Río Bobonaza, with the following exceptions: premaxilla always with 4, never 3, teeth "clustered" medially. Maxilla occasionally with 1 rather than 2 exserted "tusk" teeth. In both sexes, all premaxillary teeth usually unicuspid (cleared and stained male with medial tooth bicuspid on one side). Dentary usually with 3 (rarely 4) medial teeth tricuspid and larger than remaining teeth. Lateral cusps in specimens from Río Aguarico not as prominent as those found in population sample from Río Bobonaza, Ecuador.

See Tables 3 and 4 for vertebral counts including Weberian apparatus and terminal compound centrum and for gill raker counts.

Branchiostegal rays in three cleared and stained specimens 4 (3 on one side of one specimen). In three specimens 3 rays originate from anterior ceratohyal and 1 ray from border between anterior ceratohyal and posterior ceratohyal. In one specimen all 4 rays originate from anterior ceratohyal.

COLOR IN ALCOHOL.—Color pattern (Figure 5) similar to that of *X. macropus*; no consistent differences detected.

SEXUAL DIMORPHISM.—Tables 3 and 4 present morphometric data for specimens of *X. heterodon* arranged by sex and locality. Unequivocal differences occur in the same characters in *X. heterodon* as in *X. macropus*, including distance from snout to pelvic-fin origin (shorter in males), depth of caudal peduncle (greater in males), length of pelvic fin (much greater in males), and length of anterior anal-fin lobe (greater in males).

Analysis of covariance by sex using log transformed data for 19 morphometric characters was done for specimens from the Río Aguarico, FMNH 94940 and MEPN (uncataloged) (Table 4). Coefficients of determination were somewhat greater than found for *Xenurobrycon macropus* because of a large sample size, but again, correlation was not good, especially in the males with little variation in adult size and sexual maturation at varying sizes within that restricted range. (For discussion of male maturation size, see p. 38.) Intercepts, but not slopes, again showed significant differences ($P<0.01$ determined in a two-tailed test) between males and females for two characters which also differed in *Xenurobrycon macropus*, a greater dorsal-fin height and a longer anal-fin base in males than in females. As in *X. macropus*, hooks are absent in fins of females whereas males appear to have them in pelvic, anal, and caudal fins at least during breeding season. Complex glandular, osteological, and muscular modifications of caudal-fin region of males are absent in females.

POPULATION VARIATION.—Sample size is too small from Río Bobonaza, Ecuador, and Río Pachitea, Peru, to permit population comparison. Also, these populations were not in breeding condition as were the specimens from the Río Aguarico, Ecuador. In addition, the former two population samples were not in as good condition (scales mostly gone) as the specimens from the Río Aguarico. No population comparison was made.

ETYMOLOGY.—The name *heterodon* is from the Greek *heteros* (other or different) and *odus* or *odon* (tooth). The name refers to the mixture of tricuspid, bicuspid, and conical teeth found in this species.

Putative Pheromone Pumping Mechanisms in Glandulocaudine Fishes

Several putative pheromone pumping mechanisms of two general functional categories are found in the caudal region of glandulocaudine males. The first category, a diaphragm scale pump, has two major variations and occurs in most of the glandulocaudines. One of these two is a passive pump without much obvious muscular specialization; this pump appears to be the primitive form within the xenourobryconin glandulocaudines. A considerable amount of difference in caudal pump scale morphology is displayed by the passive pump system of various species and genera. *Iotabrycon* has a unique form of this system with obvious specialized pouch scale and musculature. The latter is not directly attached to the bellows of the pump and therefore the pump appears passively driven. The other major variation, known only in the minute subgroup B xenurobryconins, includes obvious specialized musculature and appears to be an active pump directly driven by specialized muscles attached to the diaphragm, the pouch scale, of the bellows.

The second category of pump, morphologically very different, has a valve and is formed of modified fin rays, associated scales, and soft tissue. This fin-ray pump is known only in *Mimagoniates* and evolved independently of the diaphragm pumps. One glandulocaudine genus, *Glandulocauda*, lacks a pump but does have glandular tissue distributed on the caudal-fin ray membranes.

Historical Summary

Eigenmann (1914:34) first defined the glandulocaudines and in part recognized them by the possession of "peculiar glandular scales or pouches covered by united scales" in the males. Eigenmann did not further discuss this feature. Little more was said about the caudal glands and scales until Nelson (1964a:70–74) hypothesized a pheromone function for them. For example, Böhlke (1958a:43) hypothesized that the glandulocaudines were polyphyletic, and of the caudal gland stated that all species "possess some sort of specialized scaly structure at the base of the caudal fin." Kutaygill (1960) described the histology of the secondary sexual characters of *Corynopoma riisei* but recognized no pumping mechanism. Géry (1964:8–12) described in some detail the osteology of the caudal-fin rays of "*Mimagoniates* cf. *microlepis*" but did not suggest a caudal pumping mechanism.

Nelson (1964a:70–74) described and illustrated the gross superficial anatomy of ten species in eight glandulocaudine genera and (page 142) hypothesized a sexual pheromone function for the glandular tissue. Nelson (1964a:142) also suggested that in *Coelurichthys tenuis* (*Mimagoniates lateralis* of the present paper), a caudal-fin movement that he termed "Dusting" appears to be

> ideally suited to wafting an odorous substance from the caudal gland to the region of the female's head, and inspection of the caudal morphology in this species reveals that it would be fitted for the purpose. Two fin rays are modified to form opposing halves of a tube and are so arranged that the edge of one fits inside the other (fig. 3,*F*), so that any differential movements of the two fin rays will cause them to operate as a bellows. [He also postulated that the caudal gland] produces a substance which when directed toward the female by this bellows during Dusting, increases the probability that she will Pair.

Weitzman (1975:409) briefly described courtship activity of *Corynopoma riisei* and *Pterobrycon myrnae*. In the original unpublished English version of this article he reported that during "Extending" (defined under the term "Extending Paddle" for *Corynopoma* by Nelson, 1964a:95), among other activities, the male of both these species "Tail Beats" toward the female. Tail-beating was described for *Mimagoniates microlepis* and *Mimagoniates lateralis* by Nelson (1964a:90). Tail-beating in *Corynopoma riisei* is different from "Twitching" and "Shaking" described by Nelson (1964a:90) and also observed by us. In tail-beating by *Corynopoma riisei* the male "flaps" his tail fin toward the female but with less of the V-shaped body action described for *Mimagoniates* species as illustrated by Nelson (1964a:87, fig. 6). During this activity the dorsal and anal fins are also maximally extended, and in *Corynopoma* the opercle is extended toward the female; in *Pterobrycon* elongate, specialized epaxial scales are extended toward the female. The remarks about tail-beating were eliminated from the German text by the editor. However, this extending and tail-beating activity is illustrated by Weitzman (1975) for *Corynopoma riisei* (bottom figure, page 406) and for *Pterobrycon myrnae* (bottom figure, page 408). It is hypothesized here that during tail-beating the male propels one or more pheromones toward the female's head. Nelson (1964a:91, fig. 10*b*) also illustrated a male *Corynopoma* in tail-beating activity. No accurate record of the number of beats per second is available, but the number is relatively low, only a few per second. Nelson (1964a:90) states that "Dusting" (a specialized form of tail-beating?) is confined to *Mimagoniates* (= his *Coelurichthys*) among the glandulocaudines he examined; he did not record tail-beating for *Corynopoma.* The "Dusting" activity described for *Mimagoniates lateralis* by Nelson (1964a:89, figs. 8c, 94) is also probably a specialized form of tail-beating. Tail-beating in several behavior patterns occurs not only in glandulocaudines but in other characiforms as well. We have observed it during lateral display in several species of *Nannostomus* (Lebiasinidae) and *Hyphessobrycon* (Characidae). Sometimes the beating is in head-to-facing-tail position; at other times it may be in tail-to-tail and head-to-head position. The behavior needs further study, but in the case of the glandulocaudines it seems suited for propelling a pheromone toward the female's head. We expect that tail-beating activity associated with courtship and pheromone delivery to the female may occur in a variety of specialized forms in various glandulocaudine taxa.

Nelson (1964a:142) states: "A superficial inspection of courtship in *Corynopoma, Pseudocorynopoma, Glandulocauda* [*inequalis*] [=*Mimagoniates inequalis* of the present study], or *C. microlepis* [here = *Mimagoniates microlepis*] reveals no striking features that might be correlated with caudal morphology." He goes on to point out that a more penetrating analysis does reveal a correlation. In a letter from Nelson to the senior author dated 22 January 1963, Nelson suggests a function for the caudal gland.

> [In] *Mimagoniates,* especially *barberi* [= *lateralis* of the present report], the male fans the female's head with his caudal as with a feather duster [hence "Dusting," of Nelson, 1964a: 94]. Similar things occur in other species, but are much less pronounced, so much that I at first missed it completely in *Corynopoma.* My idea is that the gland secretes an excitatory substance, which he wafts toward the female during courtship. The elaborate pouches prevent unnecessary waste and as a result of the specialized caudal movements of courtship may act then as a bellows.

Clearly Nelson here conceived of an economical mechanism for production of a sexual pheromone in the male and a method for its transport to the female. We believe his hypothesis has much merit and explore it below in conjunction with a more detailed review of the anatomy of caudal structures.

Atkins and Fink (1979) described and discussed the histology of the glandular caudal tissue in *Corynopoma riisei.* They hypothesized a sexual pheromone substance in the caudal gland and noted that males placed in aquaria without females soon have hypotrophied glands, but that when they are returned to aquaria containing females the glands again become hypertrophied. Liley (1982:28, 32) and Liley and Stacey (1983:10, 12), based on the literature, have briefly called attention to possible sexual pheromone function in the caudal glands of glandulocaudine characids. Weitzman (1982, 1985) has noted the existence of and briefly described the passive and active putative pheromone diaphragm pumps in glandulocaudines, especially the muscular pump of the xenurobryconins.

Mahnert and Géry (1984:503) briefly described parts of the osteology of male-*Xenurobrycon macropus* and on page 505 noted that the base of the eleventh caudal-fin ray (=

their eighth ray of the ventral caudal-fin lobe) is movable and bears strong musculature. They indicate that this musculature extends to neighboring fin rays and assumed that movement of the base of the eleventh ray might be involved with expelling the glandular secretion. They presented no concept of a muscular diaphragm pump.

Caudal Pump Morphologies and Putative Function

THE DIAPHRAGM SCALE PUMP

All glandulocaudine species, except those in the genera *Planaltina*, *Acrobrycon*, and *Diapoma*, have the caudal gland and associated structures confined to the males. The passive diaphragm scale pump consists of an epidermal invagination between the fin rays and the squamation, forming a sac or pouch usually located at the base of the ventral caudal-fin lobe. The sac is posteriorly or posteroventrally open to surrounding water, and glandular tissue occurs in the vicinity of the opening, especially on the fin-ray side of the pouch. In *Argopleura* and other xenurobryconins there appears to be a large amount of glandular tissue just inside the pouch opening on the medial wall of the pouch. Among species and groups of glandulocaudines there is much variation in the placement of the pouch and in the form, size, and location of the scales covering its lateral surface. For example, the relatively primitive xenurobryconin glandulocaudine *Agropleura* has the pouch mostly covered by a terminal lateral-line scale and a scale from a row just ventral to the lateral-line scale row (Figures 8, 9). Other glandulocaudines, such as *Corynopoma riisei* (Figure 16) and *Gephyrocharax atricaudatus* (Figure 17), have more ventrally placed scales on the lateral wall of the pouch. *Diapoma speculiferum* (Figure 15) has several somewhat hypertrophied scales covering the lateral wall of the pouch instead of one large scale and additional smaller scales.

This type of pheromone-associated organ may function in a similar manner in all glandulocaudine species that possess it. We hypothesize that it works as a passive pump in association with tail-beating. If one takes a freshly killed male *Corynopoma*, *Hysteronotus*, or *Gephyrocharax* and bends the tail while the fish is held under water, the scale or scales on the lateral wall of the pouch, which are on the concave side of the caudal fin, buckle outward, drawing water into the pouch. Releasing the tail, allowing it to align with the long axis of the fish, causes the scale to resume a flatter shape, collapsing the pouch and forcing water out over the glandular tissue. The apparatus thus appears to act like a bellows without a valve and only one opening. If the pouch and scale operate this way during tail-beating, the motion of the tail and the subsequent passive pumping action of the caudal pouch may increase the rate or focus the direction of the dissemination of pheromone substances into the water around the tail fin. During tail-beating in *Corynopoma* and *Pterobrycon*, the male bends his tail predominantly toward the female and bends it more slowly and to a lesser extent in the reverse direction. The pouch on the side of the fish away from the female would be much less active during tail-beating because there is little tail bending in the direction that would expand that pouch. This presumably could conserve pheromone substances on the side of the male away from the female during tail-beating. Thus glandulocaudine males may physically activate their caudal glands only, or at least to a greater extent, on the side facing the female. *Corynopoma* and *Pterobrycon* irregularly will alternate sides facing the female during courtship and tail-beating. Although not well described in the systematic literature, males of some glandulocaudine species may have part of the dorsal and ventral tail lobes separate due to interruption of the interradial membrane. Thus the fin lobes may be moved independently. This feature, tail-beating, and pheromone propagation may be related in some synergistic way to increase the efficiency of pheromone communication, but the production of pheromone and the detailed function of these morphological features remain speculative.

Another, more elaborate, kind of diaphragm-scale pumping mechanism is found in *Iotabrycon praecox* (Figures 2, 10, 23, 44, 45, 68). This pumping mechanism is similar to that just described, but the opening of the sac and the associated large scale are uniquely complex (Figures 10, 23). The glandular tissue is located around the opening of the pouch but does not extend into the elongate posteroventral process of the scale. The pouch is primarily located deep to the major fimbriated area of the scale and the pouch opening occurs along the ventral fimbriated border of the main body of the scale. The parallel fimbriae of the dorsal scale lobe lateral to the pouch (apparently hypertrophied scale lamellae separated by radii, compare Figures 23, 32) are joined by membrane so that the lateral wall of the pouch is very expandable in a lateral direction. This species has its dorsal and ventral caudal-fin lobes largely connected by a membrane. Exactly how the caudal fin of *Iotabrycon* operates in tail-beating is unknown, but presumably the structure is used during courtship to somehow bring pheromone substances to the female. For example, the hypertrophied epaxial and hypaxial muscle mass on the dorsal caudal-fin lobe may increase the force of caudal movement (e.g., sculling). This increase in turn may compensate for the greater water resistance that may affect the caudal pump of this small fish (see the following discussion of water resistance in the small pumps of subgroup B xenurobryconins).

A second type of caudal pheromone diaphragm pump is found in *Xenurobrycon, Scopaeocharax*, and *Tyttocharax*. Its physical appearance has been described above in some detail for *Xenurobrycon macropus* (p. 77–83). Also, various aspects of the structure have been described above under apomorphies 27–37, subgroup B; 47–50, *Xenurobrycon*; 55–59, subgroup C; and 61, *Scopaeocharax*.

Parts of the structure are extensively illustrated here for various species of *Xenurobrycon, Scopaeocharax*, and *Tyttocharax*, but reference to Figures 11–14, 24, 30, 46, 47 are especially helpful in understanding the structure. Briefly, the epidermal pouch is located medial to the middle and posteroventral regions of the enlarged pouch scale and opens to the surrounding water along the fimbriated posteroventral border of the scale. Part of this scale flares slightly laterally. In that vicinity the fimbriae are especially fine and the membrane between them highly distensible. The greatest concentration of hypertrophied gland cells occurs around and just inside this opening as in *Argopleura*. The scale is bound to fin rays 10 and 11 by one or two ligaments. Specialized interradialis-b muscle fibers originate along the base and unciform process of fin-ray 11 and insert in roughly a semicircle near the border of the posterior three-quarters of the pouch scale. Interradialis-a muscle fibers originate near the bases of fin rays 12–17 and insert on the unciform process of ray 11 (Figures 11–14, 46, 47). The distal portions of the dorsal-lobe caudal-fin rays pass to one side or the other of the ventral-lobe caudal-fin rays (Figure 67).

We propose that many of these modified structures of the male caudal fin may serve as a pumping mechanism increasing the rate of dissemination of a pheromone or pheromones into the surrounding water from glandular tissue situated in and around the mouth of the pouch or sac. We suggest that the boundary layer effect, in which the velocity of flowing water decreases the closer the water is to a substrate, reaching virtually zero at the boundary (Leyton, 1975:5), may be associated with the evolution of the directly driven muscular pump. Water that flows through relatively small tubes or into small sacs, such as the small pumps of subgroup B xenurobryconins, is limited to those boundary layers where greater energy is required to increase water velocity. Greater energy would not be needed in the larger pumps of the larger glandulocaudines. In addition, a relative increase in water turbulence, which occurs at orifices of small size (Leyton, 1975:19), may produce additional water flow retardation. Thus, in fishes the size of the minute xenurobryconins, the energy needed to make water flow in the caudal pump may be such that the passive mechanism in the form present in larger glandulocaudines would not be effective. Additional energy may be needed, and in subgroup B xenurobryconins may be supplied by the modified interradialis muscles. The relatively large size of the pump and diaphragm scale in relation to body size possessed by miniature glandulocaudines compared to those present in the larger glandulocaudines also may compensate for decreased flow and increased water turbulence.

The caudal pump may function in the following manner: the fan-shaped interradial muscle bundle, interradialis-b, when contracted, may cause the scale to buckle laterally and thus expand the volume of the sac internal to the scale. This would cause water to enter the sac and pass over the associated glandular tissue. Relaxation of this muscle presumably would allow the natural resilience of the scale to bring the scale back to its undeformed state, forcing water out of the sac and again over the glandular tissue. The scale presumably acts as a movable diaphragm, pumping water in and out of the sac and over the glandular tissue. Other movements used in either tail-beating or head-to-tail lateral display activity may aid in pumping water into and out of the caudal sac. The posteroventrally directed interradialis muscle, "interradialis-a" (Figures 46, 47), may act to stabilize the sigmoid ray (principal ray 11; p. 82) during contraction of the fan-shaped interradialis-b, as well as to control a pivoting or rocking motion of the sigmoid ray around its articulation with hypural 2. The extensive interradialis fibers of dorsal caudal-fin rays 7 and 10 probably cause exaggerated sculling movements, with rays 7 to 10 passing to one or the other side of the less mobile rays of the ventral caudal-fin lobe. The radii of the large scale may facilitate bending of the scale during normal swimming as well as during pumping action. The platelike projections on each side of the eighteenth principal caudal-fin ray in *Xenurobrycon macropus* may act as deflecting devices directing water bearing the pheromone towards the female.

THE FIN-RAY PUMP

The second type of glandulocaudine pump, the one mentioned by Nelson (1964a:142) on page 95, involves modifications of scales of the base of the dorsal caudal-fin lobe and modification of principal caudal-fin rays 8 to 13 and especially 11 and 12 (Figure 19 of *Mimagoniates microlepis*). This caudal mechanism will be treated in more detail in a paper on *Glandulocauda* and *Mimagoniates* by Menezes and Weitzman in preparation. Briefly, the mechanism consists of a series of about 5 to 11 dorsal lobe scales which together form a single flap extending posteriorly and ventrally lateral to the proximal parts of principal caudal-fin rays 8 to 12. A broadly open pouch or pocket lies between this flap and fin rays 8 through 11. The opening occurs along the entire ventral border of these scales. In histological sections apparent secretory cells form heavy concentrations in the scale pouch or fold. Glandular cells are also widely distributed on the fin but appear most concentrated around these modified scales and associated fin rays.

A second pouch or pocket occurs between the highly modified seven to twelve or so basal segments of the ray halves of principal caudal-fin rays 11 and 12. These segments are expanded and curved so that their opposing faces form the concave walls of the pouch. Rays 9, 10, and 13 are also modified in support of this pouch or tubular pump. Glandular tissue is not apparent inside this fin-ray pouch but does occur around its posterior opening. The structure is bilateral. Each pouch is open along the lateral borders of the fin-ray segments. This opening is divided into an elongate anterior portion and a smaller posterior portion by the expanded segments of ray 11. In life, the soft tissue around the openings restrict their extent, but they do remain continuous with each other. During ventilation of the pouch the narrow central part between the major openings is the first area to close during compression and the last to open during expansion. When the caudal fin is flexed away from the pouch being observed, the volume of the contents of the pouch decreases and the anterior portion of the opening closes. When the fin is flexed toward the pouch, the volume of the pouch expands and the anterior portion of the opening expands widely. The posterior portion of the opening remains open during all flexing activity. Nelson referred to the fin-ray mechanism as a bellows, and the pump is a type of bellows, one with a valved opening in the proximal and middle portions. The anterior portion of the opening closes as the pouch is compressed and opens as the pouch expands, while the smaller posterior portion of the opening remains open at all times. Therefore, we would suggest that the predominant flow of water is into the anterior portion of the opening and out of the posterior portion of the opening. A small amount of water might enter through the posterior opening only when the pouch is being expanded. The interradialis muscles are well developed on all fin rays and the other caudal musculature is quite robust but not greatly modified. Direct muscular action on the fin rays as well as the general bending of the fin during tail-beating may be involved in driving this pump.

Glandulocauda, apparently the closest relative of *Mimagoniates*, does not have a caudal fin ray pump and appears the more primitive morphologically. The fin-ray pump of *Mimagoniates* apparently evolved independently of the diaphragm scale pump present in other glandulocaudines.

Summary

The Xenurobryconini is corroborated as monophyletic by five synapomorphies, providing a new diagnosis. The tribe includes *Argropleura* from the Magdalena and Cauca basins in Colombia, *Iotabrycon* from the Guayas basin in Ecuador, and *Xenurobrycon*, *Scopaeocharax* (new), and *Tyttocharax* all from the Amazon basin. *Xenurobrycon* is also found in the Paraguay-Paraná basin.

Subgroups and genera of the Xenurobryconini are corroborated by apomorphies. Seventy-one apomorphies were used in this treatment, many based on secondary sexual characters of the males and many based on reductive characters associated with small size in the adults of *Iotabrycon*, *Xenurobrycon*, *Scopaeocharax*, and *Tyttocharax*. A key to the groups and genera is presented.

The phylogenetic analysis, in part, is a study of the congruence of innovative characters, such as features associated with the caudal gland, and reductive characters, such as various losses of portions of the laterosensory canal system. Both kinds of evolutionary change may be associated with miniature size and with the hydrodynamics of reduced water flow in small tubes, such as the laterosensory canals and caudal pheromone pumps. We find that the two kinds of characters usually are congruent and corroborate a single phylogenetic hypothesis. However, most of the homoplasies that we detected are reductive laterosensory system characters and we suggest that these characters, apparently related to size at maturity, maybe reversible and therefore labile in the studied taxa.

Xenurobrycon macropus from the Paraguay-Paraná basin is redescribed and two species, *Xenurobrycon pteropus* from Fonte Boa, Amazonas, Brazil, and *Xenurobrycon heterodon* from the upper Amazon basin in Ecuador and Peru, are described as new. A key to the species is included.

The distribution of the Xenurobryconini is reviewed and an area cladogram of the major subgroups is presented. Three areas of endemism are discussed, the Magdalena plus the San Juan basins of Colombia, the Guayas basin of Ecuador, and the Amazon plus the Paraguay–lower Paraná basins.

Caudal pheromone pumping mechanisms are described for several glandulocaudine groups. There are two major types, one of which has several forms. One type consists of a diaphgram pump. The diaphragm is formed of a large scale or scales lateral to a sac or pouch. The pouch has a single posterior opening surrounded by glandular tissue that presumably produces a pheromone. In most instances the pump may work passively as a result of tail-beating during courtship. In one miniature xenurobryconin, *Iotabrycon*, this passive pump has become associated with highly modified caudal musculature. In three

miniature xenurobryconin genera, *Xenurobrycon*, *Scopaeocharax*, and *Tyttocharax*, the pump appears to be directly driven by modified interradialis muscles, which are inserted along most of the posterior border of the scale diaphgram. This we call an active muscular pump. It may be driven in association with tail-beating or perhaps indepenent of tail-beating.

An entirely different type of caudal pheromone pump is present in the nonxenurobryconin glandulocaudine genus *Mimagoniates*. This pump is an elongate chamber continuously open laterally and formed primarily by modified fin rays rather than scales. The anterior portion of the chamber opening appears to act in an intake valve, and the posterior portion always remains open. We postulate that this pump works by taking water into the anterior portion of its opening, closing that opening (and its connection with the posterior opening), compressing the resulting chamber and forcing water out the posterior opening. Glandular tissue is associated with the posterior opening as well as with the caudal fin rays and is especially concentrated medial to a flap of tissue formed of modified scales just dorsal to the pump mechanism.

In Appendix 3 hypotheses of the monophyly of the Glandulocaudinae are reviewed and it is concluded that insufficient information is currently available to either support or refute a hypothesis of the monophyletic origin of the subfamily. There do, however, appear to be monophyletic groups within the subfamily.

Several hypotheses associated with the concept of internal fertilization in all glandulocaudines were advanced by Nelson (1964a). These are reviewed in Appendix 3 and it is noted again that insufficient information is available to corroborate or reject these hypotheses for all members of the subfamily. Nelson (1964a) suggested that in glandulocaudines internal fertilization and a habitus of feeding at the water's surface are evolutionarily associated. New evidence suggests that the glandulocaudines may not be surface-dependent for food any more than other tetragonopoterine characids. Furthermore, most glandulocaudines are not known to be internally fertilized and the hypothesis that internal fertilization is typical of the group appears to have little corroboration.

Nelson (1964a) also proposed that internal fertilization in glandulocaudines evolved in association with wet-season flooding of their habitats. Based on habitats that are currently occupied by many glandulocaudines and that are subject only to ephemeral flooding, there seems to be little or no evidence for many species of the group to support Nelson's hypothesis.

Resumo

A idéia de que Xenurobryconini forma um grupo monofilético é corroborada por cinco sinapomorfias que possibilitam uma nova diagnose do grupo. A tribo inclui *Agropleura*, que ocorre nas bacias do Magdalena e do Cauca na Colômbia; *Iotabrycon*, da bacia do Guayas no Equador; e *Xenurobrycon*, *Scopaeocharax* (novo), e *Tyttocharax*, todos da bacia Amazônica. *Xenurobrycon* também ocorre na bacia Paraguai-Paraná.

Os subgrupos e gêneros de Xenurobryconini são corroborados por apomorfias. Setenta e uma apomorfias foram usadas neste contexto, muitas baseadas em caracteres sexuais secundários dos machos e outras em caracteres "reductivos" associados ao pequeno tamanho dos adultos de *Iotabrycon*, *Xenurobrycon*, *Scopaeocharax*, e *Tyttocharax*. É apresentada uma chave para os grupos e gêneros reconhecidos.

A análise filogenética é, em parte, um estudo da cogruência dos caracteres "inovadores," tais como características associadas á glândula caudal, e caracteres "reductivos," como por exemplo, o desaparecimento de várias partes do sistema látero-sensorial. Os dois tipos de mudança evolutiva podem estar associados à redução de tamanho ("miniaturização") e com a hidrodinâmica do fluxo reduzido de água em tubos pequenos, como os canais látero-sensoriais e as bombas de feromônio da região caudal. Nós, achamos que os dois tipos de caracteres em geral são congruentes e corroboram uma única hipótese filogenética. Entretanto, a maioria das homoplasias que nós detectamos são caracteres "redutivos" do sistema látero-sensorial e sugerimos que estes caracteres, aparentemente relacionados ao tamanho na maturidade, podem ser reversíveis e portanto lábeis nos taxons estudados.

Xenurobrycon macropus da bacia do Paraguai-Paraná é redescrito e duas espécies, *Xenurobrycon pteropus* de Fonte Boa, Amazonas, Brasil, e *Xenurobrycon heterodon* da parte superior da bacia Amazõnica (Equador e Perú), são descritas como novas. É incluida uma chave para espécies.

A distribuição de Xenurobryconini é revista e um cladograma de áreas dos subgrupos principais é apresentado. Três áreas de endemismo são discutidas: as bacias dos rios Magdalena e San Juan na Colômbia, a bacia do Guayas no Equador e as bacias do Amazonas e Paraguai–Paraná.

Mecanisomos de bombeamento de feromônio na região caudal são descritos para vários grupos de Glandulocaudinae. Há dois tipos principais, um dos quais tem várias formas. Um tipo consiste de uma bomba tipo diafragma. O diafragma é formado por uma ou mais escamas mais desenvolvidas que recobrem uma bolsa ou saco de posição lateral em relação às escamas. A bolsa tem uma única abertura posterior circundada por tecido glandular que, ao que tudo indica, produz um feromônio. Na maioria dos casos a bomba parece trabalhar passivamente como resultado do batimento da cauda durante o processo de cortejamento. Em um Xenurobryconini, *Iotabrycon*, esta bomba passiva tornou-se associada com uma musculatura caudal altamente modificada. Em três gêneros de Xenurobryconini, *Xenurobrycon*, *Scopaeocharax*, e *Tyttocharax*, a bomba parece estar directamente relacionada com músculos interradialis modificados que se inserem ao longo da maior parte da margem posterior da escama que funciona como diafragma. Este tipo especial é denominado bomba muscular ativa. Aparentemente funciona em associação com o batimento da cauda ou talvez independente dele.

Um tipo totalmente diferente de bomba caudal associada a produção de feromônio, está presente no gênero *Mimagoniates*. Esta bomba consiste de uma câmara alongada continuamente aberta lateralmente e formada primariamente por raios modificados ao invés de escamas. A parte anterior da abertura parece agir como uma válvula e a parte posterior sempre permanece aberta. Nós postulamos que esta bomba funciona sugando água para a parte anterior de sua abertura fechando-a (bem como a conexão com a abertura posterior) e comprimindo a câmara que se forma, forçando desta forma a água para o exterior pela abertura posterior. Tecido glandular existe em associação com a abertura posterior e com os raios da nadadeiras caudal e está especialmente concentrado medialmente a uma pequena aba de tecido formada por escamas modificadas situadas dorsalmente à bomba propulsora.

No Apêndice 3, duas hipóteses sobre o monofiletismo dos Glandulocaudinae são revistas e conclui-se que apesar de atualmente não existir informação suficiente para apoiar uma hipótese de origem monofilética, parece existir grupos monofiléticos dentro da subfamília.

Várias hipóteses associadas com um conceito de fecundação interna para todos os Glandulocaudinae foram propostas por Nelson (1964a). Estas são revistas no Apêndice 3 e é notado novamente que não existe informação suficiente para corroborar ou rejeitar tais hipóteses para todos os membros da subfamilia. Nelson (1964a) sugeriu que em Glandulocaudinae a fecundação interna e o hábito de alimentar-se na superfície são evolutivamente associados. Novas evidências indicam que o grupo depende da superfície como fonte de alimento em grau comparável ao de outros caracídeos da subfamília Tetragonoptrinae. Além disto, a maioria dos Glandulocaudinae parece não possuir fecundação interna e a hipótose de que este fenômeno é típico do grupo parece ter pouca corroboração.

Nelson (1964a) também admitiu que a fecundação interna nos Glandulocaudinae evoluiu em associação com a inundação de seus "habitats." Com base nos ambientes atualmente ocupados por muitos Glandulocaudinae e que são sujeitos apenas a inundações efêmeras, parece haver pouca ou nenhuma evidência que apoie esta hipótese de Nelson para muitas espécies do grupo.

Appendix 1

Glandulocaudine Specimens Examined

Specimens of more than 40 species and 17 genera of glandulocaudines used for comparative purposes in this study are listed below. For all these genera and for most of the species, alizarin red S and sometimes alizarin and alcian blue preparations were available. All are labeled C and S. Specimens of *Xenurobrycon* used in the comparative analysis are listed in the species accounts.

Acronyms used below for institutions are defined in the acknowledgments, except the following, which indicate collections in which the specimens were formerly housed: IUM (Indiana University Museum), CM (Carnegie Museum), SU (Stanford University Natural History Museum). When the term male or female is used it means the specimens are sexually mature specimens of their respective sex. When the term adult is used it means that sexually mature specimens of both sexes are present.

Acrobrycon ipanquianus (Cope). CAS 39060 (IUM 16193), C and S, 7 adults, SL 61.0–97.7 mm, from 21 specimens, SL 61.0–100.0 mm; Peru: Cuzco (bridge at San Miguel, Río Urubamba, about 13°25′S, 71°32′W; C.H. Eigenmann, Nov 1918.

Argopleura chocoensis (Eigenmann). USNM 249871, C and S, paratypes, 1 male and 1 female, SL 48.5, 45.5 mm, and USNM 76943, paratypes, 20 adults, SL 35.5–52.8 mm; Colombia: Choco (Istmina, upper Río San Juan, 05°09′N, 76°39′W); C.H. Eigenmann, 19–20 Mar 1912. CAS 39030 (IUM 12939), C and S, paratypes, 1 male and 1 female, SL 42.5, 44.5 mm, plus 15 adults, SL 42.5–50.7 mm; same locality and collection data as preceding.

Argopleura diquensis (Eigenmann). FMNH 56272, holotype, male, SL 46.3 mm; Colombia: Atlantico (Soplaviento, town on Dique de Cartagena between Cartagena and Calamar, 10°24′N, 75°08′W); C.H. Eigenmann, 11–13 Jan 1912. Following paratypes with same locality and collection data as preceding: FMNH 526273, 6 adults, SL 34.4–46.5 mm; FMNH 69690, 5, adults, SL 33.8–45.2 mm; CAS 39013, 7 adults, SL 35.3–46.9 mm.

Argopleura magdalenensis (Eigenmann). USNM 236097 (from FMNH 56264, formerly CM 5064), paratypes, 50 adults, SL 33.0–48.5 mm; Colombia: Cundinamarca (Río Magdalena, Girardot, 04°18′N, 74°48′W); C.H. Eigenmann, 9–11 Feb 1912.

Argopleura sp. ANSP 127516, C and S, 1 male and 1 female, SL 41.9, 42.3 mm, from 32 specimens, SL 30.7–44.1 mm; Colombia: Caldas (Río Mercedes, tributary of Río Miel, Río Magdalena drainage, about 05°43′N, 74°45′W); J.E. Böhlke, W. Saul, W. Smith-Vaniz, 23 Mar 1973.

Argopleura sp. USNM 235922, C and S, 1 male and 1 female, SL 44.6, 45.1 mm, and USNM 220369, 11 adults, SL 41.9–45.9 mm; Colombia: Cundinamarca (Río Magdalena basin, Río Calandaima, tributary of Río Bogota between Viota and Mesitai del Colegio, about 04°28′N, 74°31′W); F. Flores, 9 Aug 1977. USNM 220369, 11 adults, SL 41.5–47.4 mm; same locality and collection data as USNM 235922.

Corynopoma riisei Gill. USNM 235925, C and

S, 1 immature, 1 female, 4 maturing males, 3 sexually mature males, SL 27.8–35.7 mm, and USNM 231951, 52 juveniles to adults, SL 21.1–34.7 mm; Trinidad (Cemetiere Road, below bridge on road between Point Fortin and Chatham, 10°07′N, 61°44′W); R. Bruce, 15 Mar 1982. USNM 231949, 43 juveniles to adults, SL 19.0–36.9 mm; Trinidad (central region, Tunapuna River at El Quemada Road, about 10°38′N, 61°24′W); R. Bruce, 25 Feb 1982. USNM 235923, C and S, 3 males, 1 female, SL 36.8–41.2 mm, and USNM 235924, 12 adults, SL 34.3–45.3 mm; Venezuela: Sucre (Los Barrancas, Río Manzanares, between Cumaná and Cumanacoa, 10°22′N, 65°05′W); F. Mago-Leccia, S. Weitzman, and party, 2 Mar 1977. USNM 221171, C and S, 2 males, 1 female, SL 35.6–40.5 mm, and USNM 216893, 20 juveniles to adults, SL 19.6–41.5 mm; Venezuela: Carabobo (hacienda Monte Sacro, Río Chirgua, about 09°34′N, 67°45′W); M.V. Ramirez, 24 Sep 1959. CAS(IUM) 13180, paratypes of *Stevardia aliata* Eigenmann, 3 males, 3 females, SL 42.5–47.3 mm; Colombia: Meta (Río Negro near Villavicencio, Río Negro tributary to Río Meta, about 04°10′N, 73°43′W); M. Gonzales, 1914. CAS(IUM) 13720, 20 juveniles to adults, SL 19.5–48.2 mm; Colombia: Meta (Barrigon, town next to Río Humea, tributary to Río Meta and flowing from Villavicencio, 04°10′N, 73°01′W); M. Gonzales, Mar 1914.

Diapoma speculiferum Cope. USNM 236094, C and S, 3 males, 2 females, SL 29.2–32.9 mm, and USNM 221160, 5 juveniles to adults, SL 20.5–28.1 mm; Brazil: Rio Grande do Sul (Rio Forqueta at Marquês de Souza, 29°19′S, 52°05′W); H. Britski, N. Menezes, S. Weitzman, M. Weitzman, R. LaCorte, 20 Sep 1977. USNM 221155, 1 male, 1 female, SL 44.3, 45.5 mm; Brazil: Rio Grande do Sul (Rio Forqueta, Fão, on road between Lajeado and Passo Fundo, 29°12′S, 52°14′W); N. Menezes, S. Weitzman, M. Weitzman, 7 Dec 1979. USNM 221154, 10 juveniles to adults, SL 21.6–33.3 mm; Brazil: Rio Grande do Sul (Arroio Grande where it passes under highway [BR116] between Pelotas and Jaguarão, ~1 km from city of Arroio Grande, 32°14′S, 53°50′W); N. Menezes, S. Weitzman, M. Weitzman, 14 Dec 1979.

Diapoma terofali (Géry). USNM 235927, C and S, 1 male, 1 female, SL 40.6, 41.3 mm, and USNM 236275, 2 adults, SL 38.7, 39.2 mm; Uruguay: Artigas (laguna of Arroyo Catalan Chico, about 30°49′S, 56°22′W); R. Vaz-Ferreira, J. Soriano, 13 Jan 1960. ANSP 139721, paratype, 1 adult, SL 48.3 mm; Argentina: Buenos Aires (Canal "El Cazader," Río Lujan, tributary to Río de la Plata), J. Foerster, 12 Sep 1962. (See Appendix 2 for generic referral).

Gephyrocharax atricaudatus (Meek and Hildebrand). USNM 236086, C and S, 1 male, 1 female, SL 42.8, 47.4 mm; Panama (creek by road 13 km N of Cerro-Azul, 09°07′N, 79°16′W); H. Loftin, W. Kosan, 27 Aug 1962. USNM 78533, paratypes, 33 juveniles to adults, SL 23.4–44.1 mm; Panama: Canal Zone (Frijoles, 09°10′N, 79°48′W); S.E. Meek, S.F. Hildebrand, 14 Mar 1911.

Gephyrocharax caucanus Eigenmann. FMNH 56012, holotype, female, SL 48.8 mm, and USNM 81921, paratypes, 3 females, SL 44.5–50.1 mm; Colombia: Caldas (Cartago, Río Viejo, Río Cauca drainage, 04°45′N, 75°55′W); C.H. Eigenmann, 22–23 Feb 1912. USNM 120156, 1 male, SL 36.3 mm, and USNM 121289, 1 male, SL 39.6 mm; Colombia: Vale de Cauca ("upper Río Cauca tributaries," ca 03°30′N, 76°30′W); C. Miles, Oct 1942.

Gephyrocharax chocoensis Eigenmann. FMNH 56016, holotype, male, SL 48.2 mm, and FMNH 56017, paratypes, 10 adults, SL 38.6–51.6 mm; Colombia: Choco (Istmina, upper Río San Juan, 05°09′N, 76°39′W); C.H. Eigenmann, 19–20 Mar 1912.

Gephyrocharax intermedius Meek and Hildebrand. FMNH 8945, holotype, male, SL 44.2 mm, and USNM 78556, paratypes, 26 juveniles to adults, SL 24.1–37.4 mm; Panama: (Río Chame, about 08°34′N, 79°53′W); S. Meek, S. Hildebrand, 14 Feb 1912. Note: A label in USNM 78556 in Hildebrand's handwriting states: Río Chame, Chame, Panama." Apparently the type locality is therefore the Río Chame at the town of Chame, although not listed this way in Meek and Hildebrand (1916:278) and Hildebrand (1938:254).

Gephyrocharax major Myers. CAS(IUM) 17289, "cotypes," 23 adults, SL 42.0-54.1 mm; Bolivia: Beni (Río Beni, Rurrenabaque, 14°27'S, 67°34'W); N.E. Pearson, Oct 1921.

Gephyrocharax melanocheir Eigenmann. FMNH 56049, holotype, male, SL 34.7 mm; FMNH 69554, paratypes, 9 adults, SL 30.5–39.8 mm; and FMNH 56050, paratypes, 6 adults, SL 28.8–35.9 mm; Colombia: Cundinamarca ("Bernal Creek" (=vernal creek?), tributary to Río Magdalena, near Honda, about 05°12'N, 74°32'W); C.H. Eigenmann, 28 Jan 1912.

Gephyrocharax sinensis Dahl and Medem. ICN 749, 80 juveniles to adults, SL 16.2–41.6 mm; Colombia: Cordoba ("upper" Río Sinu), G. Dahl, Dec 1950.

Gephyrocharax sp. USNM 236104, C and S, 3 males, 2 females, SL 34.2–39.8 mm; Panama: (Río Tebarico, ~4.8 km W of Llano de Piedra, 07°40'N, 80°35'W); H. Loftin, E. Tyson, 30 Sep 1961.

Gephyrocharax valencia Eigenmann. USNM 257494, C and S, 1 male, 1 female, SL 33.3, 33.9 mm; Venezuela: Guarico (Río Guarico, 6 km SW of Calabozo, 08°53'N, 67°28'W); F. bond, 13 Feb 1938. USNM 121325, 5 adults, SL 31.0–37.1 mm; Venezuela: Aragua (Río Guarico drainage, between Sebastion and San Casimiro, between 09°54'N, 67°11'W and 10°00'N, 67°01'W); L.P. Schultz, G. Zuloaga, B. Phelps, 12 May 1942.

Gephyrocharax venezuelae Schultz. USNM 236087, paratypes, C and S, 2 males, 1 female, SL 30.5–34.8 mm, and USNM 121366, paratypes, 122 juveniles to adults, SL 20.4–38.0 mm; Venezuela: Zulia (Río Negro, tributary to Río Santa Ana, below mouth of Río Yasa, a tributary of Río Negro, 09°49'N, 72°32'W); L.P. Schultz, 2 Mar 1942.

Gephyrocharax whaleri Hildebrand. USNM 106513, holotype, male, SL 39.0 mm; USNM 235926, paratypes, C and S, 1 male, 1 female, SL 39.5, 41.9 mm; and USNM 109276, 39 juveniles to adults, SL 19.1–48.5 mm; Panama (Río Chame and several nearby smaller coastal streams crossing road between Campaña and La Venta, about 08°35'N, 79°52'W); S.F. Hildebrand, F. Whaler, 10 Mar 1937.

Glandulocauda melanogenys Eigenmann. USNM 236093, C and S, 1 female, 1 male, SL 39.6, 40.2 mm; Brazil: São Paulo (small mountain stream near Alto da Serra (now Campo Grande), small railroad station ~3.5 km before railroad reaches Paranapiacaba from São Paulo, headwaters of Rio Tietê, about 23°40'S, 46°19'W); H. Britski, N. Menezes, R. LaCorte, S. Weitzman, M. Weitzman, 7 Oct 1977. FMNH 54891, holotype, male, SL 38.0 mm; FMNH 54892, paratypes, 7 males, 8 females and juveniles, SL 23.3–40.2 mm; FMNH 15025, paratype, 1 male, SL 31.3 mm; FMNH 15026, paratype, 1 male, SL 35.0 mm; USNM 177724, paratypes, 1 female, 1 male, SL 32.3, 39.9 mm; CAS(IUM) 13287, 1 male, 1 female, SL 29.0, 34.5 mm; Brazil: São Paulo (Alto da Serra, coordinates as above); J.D. Haseman, 25 Jul 1908. MZUSP 26890, 2 males, 2 females, SL 26.0–41.5 mm; Brazil: São Paulo, 2–3 km N of Alto da Serra, headwaters of Rio Tietê, about 23°50'S, 46°19'W); R. Castro, 30 Nov 1979. USNM 236415, 3 males, 4 females, SL 37.6–42.6 mm, and MZUSP 26892, 3 males, 1 female, SL 32.5–39.0 mm; Brazil (same locality and collection data as USNM 236093).

Glandulocauda melanopleura Eigenmann. FMNH 54895, holotype, male, SL 39.5 mm; FMNH 54896, paratypes, 2 developing males, SL 26.5, 29.2 mm; USNM 177725, paratype, 1 male, SL 29.4 mm; CAS(IUM) 13273, paratypes, 2 males, SL 28.8, 33.8 mm; Brazil: Paraná (Serrinha, Rio Iguaçu, 25°27'S, 49°42'W); J.D. Haseman, 22 Dec 1908. Note: The Serrinha at which Haseman collected is or was a railway junction along the Rio Iguaçu. The junction is between Palmeira to the NW, Lapa to the S, and Curitiba to the NE. It is not the Serrinha located at 25°42'S, 49°34'W, about 16 air km NE of Lapa.

Hysteronotus hesperus Böhlke. USNM 236105, C and S, 1 male, SL 55.9 mm, aquarium specimen label says imported from Colombia, 1977. USNM 164056, holotype, male SL 74.0 mm, and ANSP 75912, paratype, 1 male, SL 80.5 mm; Ecuador: Napo-Pastaza (Río Pucuno, tributary to Río Suno, a tributary of Río Napo, apparently near 00°46′S, 77°12′W); M.E. Olalla, Nov 1950.

Hysteronotus megalostomus Eigenmann. USNM 236400, C and S, 2 males, SL 28.9, 31.9 mm; ANSP 149545, 1 male, 1 female, SL 29.3, 31.3 mm; USNM 236339, 1 female, 1 male, SL 29.7, 31.4 mm; CAS 51095, 4 males, 3 females, SL 29.0–41.8 mm; Brazil: Minas Gerais (3–4 km NW of Lagôa Santa, 19°37′S, 43°58′W); P. de Miranda-Ribeiro, A. Carvalho, G.S. Myers. Note: Myers (1953:137) and Böhlke (1958a:39) cite 3–4 miles NW instead of kilometers. The label in the bottle gives "km" instead of miles. See also Weitzman and Thomerson (1970:148) The label also states "1947" as the year of collection but Myers (1943:104) indicates "Oct 1942" for this collection. FMNH 54889, holotype, SL ~34.0 mm (adult specimen in very poor condition); FMNH 54890, paratypes, 2 ?juveniles, SL 19.7, 21.0 mm; CAS (IUM) 13171, paratypes, 2 adults, SL 30.3, 31.0 mm; CAS(IUM) 13291, paratypes, 2 adults, SL 23.4, 26.1 mm; Brazil: Minas Gerais (creek, tributary to Rio das Velhas, ~4.8 km from Sete Lagoas, Rio São Francisco drainage, about 19°26′S, 44°14′W); J.D. Haseman, 10 May 1908.

Hysteronotus myersi Weitzman and Thomerson. USNM 235929, C and S, 1 male, SL 44.2 mm, and USNM 235928, 1 male, SL 44.0 mm; Peru: Huanuco (Quebrada Pijuayal, tributary to Río Pachitea, about 08°50′S, 74°42′W); Cambridge University Expedition, 1968. USNM 203697, holotype, male, SL 49.0 mm, and USNM 203698, paratypes, 6 females, SL 25.3–32.4 mm; Peru: Huanuco (small stream tributary to Río Pachitea, tributary to Río Ucayali, at NE limits of Tournavista, about 08°58′S, 74°45′W); J. Thomerson and party, 23 Aug 1964.

Iotabrycon praecox Roberts. USNM 235946, C and S, 3 males, 3 females, SL 14.8–21.8 mm; USNM 216802, 10 males, 33 immatures and females, SL 14.2–19.3 mm; USNM 216803, 8 females, 8 males, SL 15.5–18.5 mm; Ecuador: Los Rios (isolated pool of Río Palenque, tributary of Río Vinces, at Centro Cientifico, about 01°26′S, 79°44′W); G. Glodek, 13 Jul 1975. USNM 236064, 22 immatures to adults, SL 12.4–17.7 mm; Ecuador (same locality as USNM 216803); G. Glodek, Nov 1978. MCZ 48659, paratypes, C and S, 2 males, 1 female, SL 16.2–18.8 mm (Roberts' measurements); Ecuador: Los Rios (isolated pool, Río Nuevo where it flows into Río Vinces, 1 km upstream from Vinces, 01°32′S, 79°54′W); T. Roberts, 5 Nov 1971.

Landonia latidens Eigenmann and Henn. MCZ 48663, C and S, 1 male, SL 36.1 mm; Ecuador: Los Rios (Río Vinces at Vinces, 01°32′S, 79°45′W); T. Roberts, 5 Nov 1971. MCZ 48664, C and S, 5 immatures to adults, SL 25.6–42.1 mm; Ecuador: Los Rios (Río Cristal, 16 km E of Babahoyo, 02°08′N, 79°23′W); T. Roberts, 6 Nov 1971.

Mimagoniates barberi Regan. USNM 179827, lectoparatypes, 1 female, 1 male, SL 25.8, 29.5 mm; Paraguay: Paraguari (Arroyo Yâca (=Yhaca) "near Estacion Caballero"; Arroyo Yhaca is at 25°39′S, 56°53′W, Caballero is at 25°40′S, 56°49′W); A. Barbero, collection date unknown, sometime before Nov 1907. UMMZ 205420, 2 males, 5 females, SL 23.6–34.5 mm; Paraguay: San Pedro (Rio Aguaray-mi at bridge on dirt highway 2.1 km N of junction with easterly road to Capitan Bado, about 23°33′S, 56°34′W); J.N. Taylor and party, 22 Jul 1979. UMMZ 205417, 1 juvenile (smallest), 2 females, SL 17.6–25.4 mm; Paraguay: Canendiyu (small arroyo tributary to Arroyo Curuguaty, ~5.3 km by dirt road NNW of Curuguaty, 24°23′S, 55°42′W); J.N. Taylor and party, 19 Jul 1979. UMMZ 205418, 1 juvenile, 1 female, SL 15.9, 26.7 mm; Paraguay: San Pedro/Canendiyu (Rio Corrientes and adjacent pool, ~32.4 km W of turnoff to Curuguaty, 24°19′S, 55°59′W); J.N. Taylor and party, 21 Jul 1979. UMMZ 205415, 1 female, 1 male, SL 30.3, 32.6 mm; Paraguay:

Canendiyu (Rio Jejui, tributary to Rio Jejui-Guazu, about 41 km N of Curuguaty and 2 km S of Ygatimi, ca 24°09′S, 55°37′W); R.M. Bailey, J.N. Taylor, 7 Jul 1979.

Mimagoniates inequalis (Eigenmann). FMNH 54893, holotype, male, SL 32.6 mm; FMNH 54894, paratypes, 4 immature, SL 21.2–25.5 mm; and CAS(IUM) 13270, paratypes, 1 female, 1 male, SL 29.4, 31.6 mm; Brazil: Rio Grande do Sul (Pôrto Alegre, apparently collected from Rio Guaíba at Pôrto Alegre harbor, 30°02′S, 51°11′W); J.D. Haseman, 19 Jan 1909. USNM 236090, C and S, 5 immatures, SL 22.9–28.4 mm; Brazil: Rio Grande do Sul (Arroio Paradiso, Rio Cai drainage, 29°32′S, 51°20′W); N. Menezes, S. Weitzman, M. Weitzman, 8 Dec 1979. USNM 234161, 34 immatures to young adults, SL 13.2–30.5 mm; Brazil: Rio Grande do Sul (Arroio Passo de Cria, along Passo da Serra near Montenegro, Rio Cai drainage, 29°40′S, 51°25′W); N. Menezes, S. Weitzman, M. Weitzman, 8 Dec 1979. (See Appendix 2.)

Mimagoniates lateralis (Nichols). AMNH 4072, holotype of *Coelurichthys lateralis* Nichols, female, SL 29.0 mm; aquarium specimens without known locality. AMNH 4087, holotype of *Coelurichthys tenuis* Nichols, male, SL 30.0 mm, and AMNH 4088, second specimen (jar labeled "cotype" but specimen not called a type in Nichols (1913:152)); no locality or collection data. USNM 236081, C and S, 1 female, 1 male, SL 26.5, 27.5 mm; USNM 236088, C and S, 1 female, 1 male, SL 31.3, 31.6 mm; USNM 254259, 21 immatures to adults, SL 18.7–31.8 mm; and MZUSP 20495, 20 immatures to adults, SL 17.5–27.5 mm; Brazil: Paraná (small blackwater stream 5 km S of Guaratuba, 25°55′S, 48°37′W); N. Menezes, W.L. Fink, S. Weitzman, 28 Dec 1975. USNM 254258, 20 immatures to adults, SL 19.2–33.0 mm, and USNM 257113, 18 immatures to adults, SL 20.4–29.5 mm; Brazil: Santa Catarina (Ilha de São Francisco, Rio Vermelho in Barra do Sul, ~35 km from Joinvile, 26°14′S, 48°35′W); H. Britski, N. Menezes, R. LaCorte, S. Weitzman, M. Weitzman, 23 Sep 1977. (See Appendix 2.)

Mimagoniates microlepis (Steindachner). USNM 249880, C and S, 1 female, 1 male, SL 46.4-60.9 mm; USNM 249886, C and S, 2 males, SL 35.1-37.3 mm; USNM 254261, 10 adults, SL 35.4-61.1 mm; MZUSP 26899, 9 adults, SL 42.6-61.1 mm; Brazil: São Paulo (Rio Silva, road between Ubatuba and Taubaté, 23°23′S, 45°07′W); N. Menezes, S. Weitzman, M. Weitzman, 27 Oct 1982. USNM 257114, 6 immatures to adults, SL 25.2-42.3 mm; USNM 249886, C and S, 2 males, SL 35.1-37.3 mm; USNM 249897, 4 immatures to adults, SL 21.8-48.1 mm; Brazil: Paraná (Rio Nhundiaquara at Morretes, 25°29′S, 48°48′W); H. Britski, N. Menezes, S. Weitzman, W. L. Fink, 27 Dec 1975. USNM 236089, C and S, 2 females, 2 males, SL 31.1-45.3 mm; USNM 249890, 6 adults, SL 33.3-49.3 mm; USNM 257115, 9 adults, SL 35.0-49.9 mm; Brazil: Paraná (Rio Nhundiaquara at Morretes, 25°29′S, 48°48′W); H. Britski, N. Menezes, R. LaCorte, S. Weitzman, M. Weitzman, 24 Sep 1977. USNM 249896, 17 immatures to small adults, SL 21.5–35.6 mm; Brazil: Rio de Janeiro (stream near Cachoeiras de Macacu, Rio Macacu drainage, 22°29′S, 42°41′W); C. Cruz, O. Peixoto, S. Weitzman, M. Weitzman, 27 Nov 1979 (See Appendix 2.)

Phenacobrycon henni Eigenmann. MCZ 48660, C and S, 1 male, SL 30.2 mm, and MCZ 48661, C and S, 3 females, SL 25.5–27.7 mm; Ecuador: Los Rios (isolated pool, Río Nuevo where it flows into Río Vinces, 1 km upstream from Vinces, 01°32′S, 79°45′W); T. Roberts, 5 Nov 1971.

Planaltina myersi Böhlke. CAS(SU) 18636, holotype, male, SL 35.7 mm; Brazil: Distrito Federal de Brasilia (formerly part of Goias), ("Sarandi brook," Chapadão do Sarandy, near Planaltina, about 15°40′S, 47°45′W); C. Ternetz, 21 Sep 1923. USNM 236416, 1 immature, 1 female, 1 male, SL 19.3–40.7 mm; Brazil: Distrito Federal de Brasilia (Rio Pipiripau, Córrego Vargem de Trás, near Planaltina, about 15°40′S, 47°39′W); N. Menezes, E.K. Bastos, 01 Jun 1979. MZUSP (uncatalogued), 3 females, SL 34.8–41.2 mm; USNM 221202, 4 females, SL 39.8–43.1 mm; Brazil: Distrito Federal de

Brasilia (Córrego Pipiripau, a tributary to Rio São Bartolomeu, Rio Paraná system, ~2 km S of Planaltina, 15°40'S, 47°39'W); N. Menezes, R. LaCorte, S. Weitzman, M. Weitzman, 30 Sep 1977. USNM 258458, C and S, 1 female, SL 41.0 mm; Brazil: Distrito Federal de Brasilia (Córrego Pipiripau near Planaltina, 15°40'S, 47°39'W); E.C. Calaf, 19 Jan 1976. MNRJ 10634, 24 immatures to adults (2 males), SL 23.5–37.0 mm; Brazil: Distrito Federal de Brasilia (Córrego Fumal, where it crosses road between Brasilia and Formosa, about 15°20'S and between 47°40'W and 47°50'W); L.E. de Macedo Cordoso, 4 Nov 1982. MNRJ 10635, 13 immatures and adult females, SL 21.3–35.5 mm; Brazil: Distrito Federal de Brasilia (Córrego Fumal, where it crosses road between Brasilia and Formosa); L.E. de Macedo Cordoso, 5 Aug 1981.

Pseudocorynopoma doriae Perugia. USNM 235930, C and S, 3 males, 1 female, SL 38.8–59.5 mm; USNM 235931, 20 adults, SL 38.1–55.1 mm; AMNH 12346, 33 adults, SL 40.0–55.5 mm; Argentina: Buenos Aires (no other locality or collection data). CAS(SU) 51056, C and S, 1 female, 1 male, SL 43.0, 60.0 mm; Argentina: "La Plata River, 220 km N of Buenos Aires"; A.W.C.T. Herre, Jun 1934. Note: Km 220 N of Buenos Aires is well beyond the Río La Plata, and is in the Río Uruguay or Río Paraná. USNM 236091, 1 female, 1 male, SL 45.4, 52.5 mm; Brazil: Rio Grande do Sul (Arroio Chapéu Virado, tributary of Rio Guaíba, S of Pôrto Alegre, about 30°06'S, 51°13'W); H. Britski, N. Menezes, V. Schultz, R. LaCorte, S. Weitzman, M. Weitzman, 21 Sep 1977.

Pseudocorynopoma heterandria Eigenmann. USNM 236092, C and S, 1 male, SL 67.3 mm; Brazil: São Paulo (Salesópolis, Rio Paraitinga, 23°32'S, 45°52'W); collector unknown, 23 Apr 1975.

Pterobrycon landoni Eigenmann. FMNH 56250, holotype, male, SL 25.1 mm; Colombia: Choco (Boca de Raspadura at junction of Río San Pablo and Río Raspadura, Río Atrato basin, 05°15'N, 76°41'W); C.H. Eigenmann, 21–22 Mar 1912.

Pterobrycon myrnae Bussing. USNM 236066, paratypes, C and S, 2 males, 1 female, SL 31.7–34.8 mm, and USNM 211459, paratypes, 37 immatures to adults, SL 22.6–39.0 mm, Costa Rica: Puntarenas (Peninsula de Osa, Quebrada Banegas (=Vanegas), 0.8 km upstream from Pacific Road, ~3 air km SW of Rincon, 08°40'N, 83°31'W); N. Scott, J. Vandemeer, 1 Mar 1968. USNM 236067, paratype, C and S, 1 male, SL 33.1 mm, and USNM 211460, paratypes, 1 male, 1 female, SL 26.7, 26.9 mm; Costa Rica: Puntarenas (Peninsula de Osa, Quebrada Banegas (=Vanegas), swamp near Quebrada Banegas at Pacific Road, ~3 air km SW of Rincon, 08°40'N, 83°31'W); S. Stearns, 14 Aug 1973.

Scopaeocharax atopodus (Böhlke). ANSP 78717, paratypes, C and S, 1 female, 1 male, SL 19.2, 20.2 mm; ANSP 78714, holotype, SL 20.0 mm; and ANSP 78715, paratypes, 2 females, SL 17.9–18.4 mm; Peru: Huanuco (vicinity of Tingo Maria, Río Rondos, tributary to Río Monzon, about 09°10'S, 76°00'W); Catherwood Expedition, 29 Sep 1955. USNM 236095, C and S, 1 female, 2 males, SL 17.8–21.1 mm, and USNM 207517, 21 juveniles to adults, SL 13.7–22.0 mm; Peru: Huanuco (Río Huallaga, vicinity Universidad Agraria de La Selva, Tingo Maria, about 09°09'S, 75°57'W); W. Sherbrook, 9 Aug 1966.

Scopaeocharax rhinodus (Böhlke). ANSP 78711, paratypes, C and S, 1 female, 2 males, SL 19.2–22.4 mm; Peru: Huanuco (vicinity Tingo Maria, Río Rondos, tributary to Río Monzon, about 09°10'S, 76°00'W); Catherwood Expedition, 29 Sep 1955. ANSP 78707, holotype, SL 22.7 mm, Peru: Huanuco (Cava de Pavos, Quebrada de Puente Perez, ~0.4 km (1/4 mi) above Río Huallaga, coordinates uncertain); C.C.G. Chaplin, M. Hohn, 30 Sep 1955. ANSP 78712, paratype, 1 male, SL 24.3 mm; Peru: Huanuco (vicinity Tingo Maria, Río Bella, tributary to Río Monzon, about 09°10'S, 76°00'W); C.C.G. Chaplin, M. Hohn, 27 Oct 1955. ANSP 78713, paratype, 1 male, SL 20.9 mm; Peru: Huanuco (vicinity Tingo Maria, limestone stream, tributary to Río Monzon near "Fungus Cave," ~3.2

km (2 mi) above Río Huallaga, ca 09°10′S, 76°00′W), Catherwood Expedition, 28 Sep 1955.

Tyttocharax madeirae Fowler. USNM 222007, C and S, 2 females, 4 males, SL 13.5–17.0 mm, and USNM 179540, 26 juveniles to adults, SL 11.7–15.9 mm; Brazil: Amazonas (Rio Urubú, ~25 km from Itacoatiara on road between Itacoatiara and Manaus, about 03°07′S, 58°39′W); H. Schultz, 8–10 Oct 1958. ANSP 39305, holotype, early maturing male, SL 14.5 mm, and ANSP 39306, paratype, 1 immature, SL 11.5 mm; Brazil: Amazonas (tributary to Rio Madeira near Porto Velho, about 08°45′S, 63°55′W); E.A. Smith, Jan or Feb 1913. USNM 92961, paratype, 1 immature, SL 10.9 mm; Brazil: Amazonas (Igarapé de Candelaria, Rio Madeira), E.A. Smith, Sep 1912. MNRJ 3572, types of *Microcaelurus odontocheilus* A. de Miranda-Ribeiro (1939:362), male, SL 17.5 mm (here designated the lectotype), female, SL 14.7 mm; type locality not given. (See Appendix 2.)

Tyttocharax sp. A. MCZ 49954, C and S, 3 males, SL 17.0–18.2 mm; Ecuador: Napo (Río Napo, Mandura Cocha, near Coca, 00°28′S, 76°58′W); T. Roberts, 11 Dec 1971.

Tyttocharax sp. B. USNM 232369, 5 males, 3 juveniles and females, SL 13.1–21.4 mm, Brazil: Amazonas (Igarapé Açu 7 km downstream from Santo Antonio do Içá, Rio Solimões, 03°02′S, 67°50′W); P. Vanzolini, 20 Oct 1968. MZUSP 12411, 3 males, 16 juveniles and females, SL 12.6–18.8 mm; same locality data as preceding; P. Vanzolini, 19 Oct 1968. (See Appendix 2.)

Xenurobrycon. Stained and other specimens of the three species examined are listed in the materials section of the species accounts in this paper.

Appendix 2

Identification, Taxonomic, and Nomenclatural Notes on the Specimens Examined

Species identification of some specimens and generic referrals of some species have proved problematic. Some of our name choices and referrals differ from those previously used. Below we give reasons for our choice of names for the specimens used in this report.

Diapoma terofali (Géry). The reasons for referral of *terofali to Diapoma* instead of to *Glandulocauda* as originally done by Géry (1964) are as follows: The modified caudal scales in *Glandulocauda melanogenys* Eigenmann, the type of the genus *Glandulocauda*, and in *Glandulocauda melanopleura* Eigenmann develop from the dorsal caudal-fin lobe squamation. That of *Diapoma terofali* develops from the squamation of the ventral caudal-fin lobe as in most other glandulocaudines and in *Diapoma speculiferum*. *Glandulocauda* has no sac between the scales and the fin rays, whereas in *Diapoma terofali, D. speculiferum*, and most other glandulocaudines, a sac is present (except for species of *Mimagoniates*, which have a caudal squamation similar to that of species of *Glandulocauda*). In contrast to most glandulocaudines, except species of *Acrobrycon* and *Planaltina*, the two species of *Diapoma* have a modified caudal squamation in both sexes rather than in the male only. The reasons for placing *terofali* in *Diapoma* rather than in *Acrobrycon* or *Planaltina* are complex and are the subject of a study in progress by S. Weitzman and N. Menezes.

Mimagoniates inequalis (Eigenmann). This species is here assigned to *Mimagoniates* rather than to *Glandulocauda* as originally done by Eigenmann (1911b:169), because large, sexually mature males possess the same type of caudal finray modifications present in the other species of *Mimagoniates*. These derived structures are absent in the two species of *Glandulocauda* listed here. (See Figure 19 and p. 98 regarding the caudal morphology of *Mimagoniates*.)

Mimagoniates lateralis (Nichols). Pending completion of a review of *Glandulocauda* and *Mimagoniates* by N. Menezes and S. Weitzman, we identify all specimens listed as *lateralis* as a species of *Mimagoniates* that apparently is confined to blackwater coastal streams of eastern Brazil between Santos and the region near Joinvile.

Mimagoniates microlepis (Steindachner). Identification to species of all lots listed as *Mimagoniates microlepis* is tentative. Two names are available, *Mimagoniates microlepis* (Steindachner, 1876), type locality Rio Macacu, Rio de Janeiro, and *Mimagoniates iporangae* (A. de Miranda-Ribeiro, 1908), type locality Ribeirão das Pedras, Iporanga, Rio Ribeira drainage, São Paulo, Brazil. Until population samples of these fishes are studied by Menezes and Weitzman, we refer all these specimens to one species and use the oldest available name.

Tyttocharax madeirae Fowler. Based on an examination of the types and other specimens listed here under *Tyttocharax madeirae*, we conclude that *Microcaelurus odontocheilus* is a junior synonym of *T. madeirae*. Myers and Böhlke (1956:7) and Böhlke (1958b:319) indicate two notable differences in these nominal species. *Microcaelurus odontocheilus* was reported to have a maxilla reaching posteriorly to beneath the middle of the eye and a standard length of 30 to 35 mm. *Tyttocharax madeirae* was reported to have a maxilla extending posteriorly not further than the anterior border of the eye and to have a standard length of about 15.0 mm. Myers and Böhlke (1956:6, 7) state that the types of *Microcaelurus odontocheilus* were "cursorily examined" by Myers during 1943 in Rio de Janeiro. They further note on page 7 that notes and sketches made at the time have been lost. We find that the types of *Microcaelurus odontocheilus* are considerably shorter in standard length than Myers recalled. The larger male is a little longer than the largest specimen of *Tyttocharax madeirae* here recorded from the Rio Urubú. Adult males of *Tyttocharax madeirae* appear to reach between 15.0 and nearly 18.0 mm SL. Examination of the mouths of the types of *Microcaelurus odontocheilus* reveals why both A. de Miranda-Ribeiro (1939:362) and Myers and Böhlke (1956:7) believed this nominal species to have a long maxilla reaching posteriorly to below the middle of the eye. Apparently A. de Miranda-Ribeiro in searching with a needle for a posterior termination of the maxilla accidentally and on both sides, broke the posterior border of the second infraorbital free from the anterior border of the third infraorbital and from the orbital rim. The result looks remarkably like a posterior end of a broad and long maxillary ramus. However, the posterior maxillary ramus of *Tyttocharax* is relatively slender and short compared to other xenurobryconins and most characids. Apparently both Myers and A. de Miranda-Ribeiro assumed the freed posterior border of the second infraorbital to be the free posterior border of the maxilla. In these type specimens a short and slender maxilla is present anterior to the first and dorsoanterior to part of the second infraorbital bones on each side. The types of *Microcaelurus odontocheilus* have the maxilla not reaching the anterior border of the eye. We could find no characters that distinguish the type specimens of *Microcaelurus odontocheilus* from the types or other specimens of *Tyttocharax madeirae*. If the type locality, near Parintins, Amazonas, given for *Microcaelurus odontocheilus* by Myers and Böhlke (1956:7) is correct, the locality is well within the ranges of specimens recorded for *Tyttocharax madeirae* by Böhlke (1958b:320), Géry (1963:59), and by us herein. On page 108, the male of the two types of *Microcaelurus odontocheilus* has been designated the lectotype.

Tyttocharax species B. These specimens appear to be *Tyttocharax boehlkei* Géry (1965b:195), which may be a junior synonym of *Tyttocharax cochui* (Ladiges, 1950:308). Ladiges sent two specimens of *Tyttocharax cochui* to Myers (Myers and Böhlke, 1956:10). Ladiges (1950:305) stated that originally six specimens were imported alive to Germany from Ramon Castillo by Firma Aquarium-Hamburg in 1949. Two of these were studied by Ladiges and given to the Zoologie Staatssammlung des bayerischen Staats in Munich. Presumably the specimens given to Myers were also from the original lot of six. Myers and Böhlke (1956:10) considered *T. cochui* a junior synonym of *T. madeirae* and noted that "as evidence of the conspecificity of the two nominal forms, counts, measurements and proportions of the holotype (female) of *madeirae* and a female of *cochui* from Ramon Castillo are presented in Table 1. Besides proportions and counts, the two are alike in dentition, coloration and general appearance." Ladiges' specimens sent to Myers consist of a pair. The male was at some time partly dried but still has evidence of body and fin pigment, has all its scales, and is otherwise in good condition. It is the males of different *Tyttocharax* species that are clearly distinct. *Tyttocharax madeirae* males have large pelvic fins, which originate ventral to the midlength of the pectoral fin and extend to about the fifth branched ray of the anal fin. In *Tyttocharax cochui* males the pelvic fin originates ventral to the posterior tip of the pectoral fin and extends posteriorly only to about the origin of the anal fin. Thus sexually mature *Tyttocharax madeirae* males have much larger pelvic fins than do *Tyttocharax cochui* males. There are other differences, such as color pattern. We tentatively conclude that the species are different, pending completion of a review of *Scopaeocharax* and *Tyttocharax* by the senior author. However, *Tytto-*

charax cochui males are very similar to the male of *Tyttocharax boehlkei* as described by Géry. It is our opinion that the two names probably refer to the same species. Furthermore, both type localities are very near Tabatinga, Amazonas, Brazil. If the names refer to the same species, *Tyttocharax cochui* is the senior synonym. However, a preliminary study of many specimens of *Tyttocharax* from Peru (Río Napo) and the Rio Solimões indicates that there may be several additional, but difficult to distinguish, western Amazon *Tyttocharax* species. In contrast, all specimens from the "lower" Amazon and Rio Madeira regions seem to be *Tyttocharax madeirae.* The holotype of *T. madeirae* is a maturing male, not a female as reported by Böhlke (1956:10).

Appendix 3

A Critique of the Monophyly of the Glandulocaudinae

Stanley H. Weitzman, Sara V. Fink, and Naércio A. Menezes

Nelson (1964a) proposed an extended series of interrelated hypotheses associated with the concept of a monophyletic origin of the Glandulocaudinae. Böhlke (1958a:43) and Géry (1977:35) stated that the subfamily may not form a natural group. Mahnert and Géry (1984:512) indicated that they think the group is polyphyletic. We find no evidence of polyphyly but agree with Böhlke (1958a) and Géry (1977). However, since these authors made no attempt to reexamine Nelson's evidence and since Nelson's hypotheses in part may have much merit for certain glandulocaudine groups, we reexamine his ideas in relation to phylogenetic analysis. In the light of some new morphological and ecological information we find the situation more complex than suspected by Nelson.

Nelson (1964a) hypothesized that glandulocaudines were a monophyletic lineage on the basis of his observations on morphology, courtship behavior, and internal fertilization. His ideas may be summarized as follows.

1. All male glandulocaudines have one or more secondary sexual attributes, such as various modified caudal scales and pouches, bony fin-ray hooks in the caudal, dorsal, anal, and pelvic fins. Some have enlarged fins, modified opercular bones, and humeral scales. All of these features were assumed or, in certain cases, observed to be directly involved in specialized courtship behavior. These structures taken together apparently were assessed by Nelson as a trend indicating glandulocaudine monophyly.

2. Those glandulocaudines for which there was reliable or relatively complete courtship and spawning information were found to be internally fertilized.

From (1) and (2) Nelson assumed it highly probable that all glandulocaudines were internally fertilized and that those that were not (possibly *Pseudocorynopoma*) had secondarily lost the characteristic and were specialized in this regard. According to this hypothesis, internal fertilization could be considered a derived feature of the Glandulocaudinae, a characteristic not known for other characids. The accompanying specialized male courtship behavior and its associated specialized morphological structures were thought to have evolved so that a relatively unresponsive female would cooperate for spermatophore transfer.

3. With internal fertilization came an uncoupling of the previously simultaneous mating and spawning acts, enabling glandulocaudines to mate during times of low water when food may be less abundant but the fishes are relatively crowded and mates easy to find. Then during high water or flooding, when food is relatively abundant but mates harder to locate, spawning may take place without mating and glandulocaudine species may take advantage of the increased food supply for both adults and young. Nelson appears to have assumed this ecological-behavioral pattern was a property of at least most or all glandulocaudines.

4. Nelson further postulated that glandulocaudines evolved this capacity because their morphology (mouth and body shape) and his experience with the behavior of some species indicated that glandulocaudines were top feed-

ers, already taking advantage of the suface habitat. Nelson proposed that this allowed them easily to invade flooded areas because they were preadapted to this shallow environment.

In our view there are several questions and problems about these hypotheses and we treat them one at a time, in order, below.

1. Morphology as evidence of glandulocaudine monophyly. The single morphological character that Nelson (1964a:70) found in all the glandulocaudines he examined was presence of "thickened glandular areas [associated with the tail fin] in combination with some sort of modified scales." We agree that hypertrophied tissue of some sort is present in adult males of most species (*Diapoma*, *Acrobrycon*, and *Planaltina* may be an exception), although in most species it is concentrated on the ventral caudal-fin lobe rather than on the middle caudal-fin rays as reported by Nelson. Evidence is not at hand to indicate that the hypertrophied "glandular tissue" of various glandulocaudine subgroups is cytologically or histologically similar in ways that would allow recognition of sister group status for these taxa. Likewise there is no evidence to indicate that such tissues are nonhomologous and are independently evolved. Thus, at this time we cannot evaluate hypotheses that might use homology of glandular tissue as a synapomorphy.

We could find no aspect of scale modification that appeared to be a general property of all glandulocaudines. Not only does scale shape differ between various glandulocaudine subgroups, but modified scales are formed in some cases from scales of the ventral caudal-fin lobes, in others from a middle (lateral-line) scale, and in others from scales of the dorsal caudal-fin lobe (compare Figures 8, 11, 14–20). We cannot accept the simple attribute of "modified caudal scales" regardless of their detailed derivation and varied morphological associations as a synapomorphy.

Other "glandulocaudine" structures proposed by Nelson (1964a:146) as indicative of glandulocaudine monophyly, such as fin-ray hooks on the caudal and dorsal fins, as well as on the anal and pelvic fins, and longer dorsal and/or anal fins in the males, are present in many other characid subgroups and are not present in a number of glandulocaudines. These characters and several others, such as a deeper caudal peduncle in the mature male, are synapomorphies for one or more groups of glandulocaudine species that possess them. However, their homology and distribution among characid taxa needs study and clarification before they can be used to corroborrate hypotheses of relationship.

Nelson's behavioral and physiological evidence for monophyly was based on observations of live specimens of six species placed in what here are considered to be three genera. These species are, as Nelson called them, *Corynopoma riisei*, *Pseudocorynopoma doriae* Perugia (1891:646), *Pseudocorynopoma heterandria* Eigenmann (1914:39), *Coelurichthys microlepis*, *Coelurichthys tenuis* Nichols (1913:152), and *Glandulocauda inequalis*. In the present work the last three species are placed in *Mimagoniates*. In our view these six fishes belong to at least two of the major groups of glandulocaudines. *Corynopoma* and *Pseudocorynopoma* perhaps should be placed as part of one group and *Mimagoniates* and *Glandulocauda* as the constituents of another. Little evidence is available that supports a close relationship between these two groups or that support a relationship of either with the Xenurobryconini.

Nelson (1964a:130) found one courtship behavior common to all six species, an up-and-down movement he termed "zigzagging." He did not find this behavior in any of the other characids he observed and found no reports of it in the literature. Today this feature would be considered a synapomorphy for those glandulocaudines that have it. While "zigzagging" might provide evidence for relationship between the two groups of glandulocaudines of which the six species appear to be members, there is no positive (or negative) evidence on the behavior in other glandulocaudine groups, for example the xenurobryconins. Observations on other glandulocaudines and characids are needed before such behavior can be interpreted as a glandulocaudine synapomorphy. This is especially true since we have observed a similar up-and-down movement in the courtship of *Cheirodon dialepturus* Fink and Weitzman (1974:5), a fish currently considered unrelated to glandulocaudine characids on the basis of morphology and available data on relationships within the Characidae.

Among the glandulocaudines that Nelson studied (1964a:136, 1964b:138–142), he observed other behavioral similarities, such as temporal patterning in courtship behavior. The primary problem we find with using Nelson's behavioral data for synapomorphies to corroborate a hypothesis of glandulocaudine monophyly is that there is so little outgroup information. Thus we cannot evaluate the derived versus primitive nature of his behavioral characters. Furthermore, we cannot tell whether the characters are restricted to glandulocaudines, whether they are found in all of them, or whether the characters are widely or narrowly distributed in other characids. We have no objections to the use of what appear to be inherited behavioral characters as synapomorphies, but we would require these characters to receive the same kind of phylogenetic evaluation as morphological characters.

2. Internal fertilization as evidence of glandulocaudine monophyly. From the knowledge that *Corynopoma* definitely undergoes internal fertilization and that *Mimagoniates* appears to do the same, Nelson (1964a:130) extrapolated internal fertilization to a putative common ancestor of all glandulocaudines. Nelson (1964a:134) observed that females of *Corynopoma* can lay fertile eggs at least seven months after last having contact with a male and (1964a:84) that females of *Mimagoniates* lay eggs without the presence of a male for at least a short time after courtship is terminated. The egg-laying activity in *Mimagoniates* is somewhat similar to that activity in *Corynopoma*. We were able to confirm Nelson's observations of *Corynopoma* with live specimens in aquaria and have had females produce live eggs and subsequent young after being isolated from males for seven months. Nelson (personal communication) recently informed us that two unspecified species of *Gephyrocharax* are also internally fertilized. Breder and Rosen (1966:158–162) have reviewed the rather controversial, mostly German, aquarium literature concerning internal fertilization in *Pseudocorynopoma* and *Mimagoniates*. Reports of *Glandulocauda* in aquaria are based on *Mimagoniates inequalis*, a species previously assigned to *Glandulocauda* by most ichthyologists including Eigenmann. The breeding behavior of species of *Glandulocauda*, *G. melanogenys* Eigenmann (1911b:168), and *G. melanopleura* Eigenmann (1911b:168), have never been reported by aquarists. Except for Nelson's observations on *Mimagoniates*, reports of internal fertilization in *Mimagoniates* and *Pseudocorynopoma* are equivocal but persistent in the aquarium literature cited by Breder and Rosen (1966:158, 161, respectively), even though contested by other aquarists. In any case, it appears that *Mimagoniates* is internally fertilized and that *Pseudocorynopoma* may be internally fertilized. However, we cannot ascribe internal fertilization to all 17 putative glandulocaudine genera on the basis of Nelson's observations (1964a:136–137) of internal fertilization in two genera, *Corynopoma* and *Mimagoniates* (now three genera, including *Gephyrocharax*), and possible internal fertilization in another, *Pseudocorynopoma*. Nelson (1964a:141) in fact leaned toward the hypothesis that *Pseudocorynopoma* had reverted to external fertilization.

Bussing and Roberts (1971:179) raised the question of oral fertilization in *Corynopoma riisei*, a species of *Gephyrocharax*, *Pseudocorynopoma doriae*, and *Pterobrycon myrnae* while still admitting internal fertilization in *Corynopoma riisei*. Facultative oral and internal fertilization seems unlikely to us, and we agree with Nelson (personal communication) that the mouthing by the female of the spot on which the egg is to be laid is probably some sort of cleaning action. Nelson tells us that he has seen eggs of *Corynopoma riisei* hatch from locations that the female failed to mouth.

Roberts (1973:513) also raised objections to premature acceptance of internal fertilization in all glandulocaudines. In particular, he criticized Nelson's hypothesis that the occurrence of caudal fin-ray hooks in many glandulocaudine species indicates internal fertilization, arguing that such hooks might facilitate external fertilization as well, particularly in swiftly flowing streams. We concur with Roberts's skepticism but note that caudal-fin hooks appear to be relatively rare in characids other than glandulocaudines.

While many, if not all, glandulocaudines may be internally fertilized, we believe it is premature to accept internal fertilization as a synapomorphy indicating monophyly for the group. Nelson's sample was restricted to about 15 percent of the known glandulocaudine species and some of the major groups (based on similarities of gross morphology) are unrepresented in his sample. His hypothesis of relationship is based on an unwarranted extrapolation. Furthermore, even if all the genera were internally fertilized we would prefer to explore the accompanying derived morphology before accepting the character as a synapomorphy.

3. Wet-dry seasonal variation and internal fertilization. One part of Nelson's hypothesis regarding the evolution of internal fertilization in glandulocaudines is related to wet-dry season alternations in habitat. Nelson (1964a:132–133) postulated that during the dry season adults are concentrated in pools and streams where mates are readily available. During the wet season, when seasonal flooding takes place and many fishes are spawning, including many of the glandulocaudines, the adults are dispersed in the food-rich flood waters. Mates are harder to find and an already fertilized glandulocaudine female will have certain spawning advantages because she does not need to locate a mate in order to lay fertile eggs.

This conjecture is not supported with field observations for all glandulocaudine species. We find that glandulocaudines live in a variety of habitats, many unlike that described by Nelson. Some, for example at least two species of *Mimagoniates* and the two species of *Pseudocorynopoma,* live in slow, lowland portions of Brazilian coastal streams usually subject only to mild flooding. Such flooding is often ephemeral (less than 24 hours in duration) rather than the longer term flooding discussed by Nelson. In the coastal streams spawning appears seasonally associated with temperature and rainfall fluctuation but not with longer-term flooding typical of the lowland parts of the Amazon basin where few glandulocaudines occur. The advantages suggested by Nelson do not apply to fishes in the short coastal streams of the lowlands or in the streams near the base of the Andes. It is in these two kinds of places that most glandulocaudines have been collected.

In our opinion speculative hypotheses about ecological correlates of the evolution of morphological features, although interesting and perhaps of scientific value, are often difficult to corroborate or test. The difficulty with all such scenarios is the lack of a method for distinguishing which, if any, among them are closer to historical fact; i.e., how such hypotheses can be tested.

4. Surface feeding as a correlate of internal fertilization. Nelson (1964a:130–135) also elaborated a hypothesis that internal fertilization may go hand-in-hand with adaptation for feeding at the water's surface. He noted that most glandulocaudines have somewhat oblique mouths suitable for surface feeding and suggested that glandulocaudines, like certain surface-dwelling freshwater fishes such as many species of the Poeciliidae and Hemiramphidae, have evolved internal fertilization. Nelson implied that a habitat oriented toward the water's surface, shallow-water or flood-water breeding, and internal fertilization may be related in evolution. This hypothesis may be correct for some groups of fishes but we do not believe that it is necessarily true for all glandulocaudines, even if all are fertilized internally. We dispute one aspect of Nelson's hypothesis, namely that glandulocaudines as a whole feed at the surface more than many other groups of characids. As was recognized by Nelson (1964a:129), not all glandulocaudines have oblique mouths. For example, *Argopleura, Acrob-*

rycon, Diapoma, and *Planaltina* all have more or less horizontal, terminal mouths that are no more oblique than those of many tetragonopterines. Thus not all glandulocaudines have the physical characters commonly associated with surface feeding. We would note also that tetragonopterines display a great amount of variation in jaw orientation among species and genera.

Two of us (Weitzman and Menezes) have observed the following glandulocaudine species alive in the wild and/or in aquaria as noted below: *Corynopoma riisei* (both), *Diapoma speculiferum* Cope (1894:67) (both), *Gephyrocharax atricaudata* (Meek and Hildebrand, 1912:68) (aquaria), *Gephyrocharax venezuelae* Schultz (1944:324) (both), *Glandulocauda melanogenys* (both), *Hysteronotus hesperus* Böhlke (1958a:35) (aquaria), *Mimagoniates inequalis* (wild only), *Mimagoniates microlepis* (both), *Mimagoniates lateralis* (both), *Planaltina myersi* Böhlke (1954:267) (wild only), *Pseudocorynopoma doriae* (both), *Pseudocorynopoma heterandria* (aquaria), and *Pterobrycon myrnae* Bussing (1974:138) (aquaria). None of these species are surface-dwelling fish in the sense of most poeciliids, freshwater live-bearing hemiramphids, or gasteropelecine characids (which are apparently not internally fertilized), and only one or two may feed at the surface more than most other tetragonopterines. Most of the live glandulocaudines examined so far are either "midwater" fishes or, in the case of *Glandulocauda melanogenys,* live in proximity to the substrate in waters often over a meter in depth. It is true that in aquaria adult *Corynopoma riisei* learn to stay more or less near the surface during feeding time or when their aquarium is approached by humans, but many nonglandulocaudine characids that in the wild live in the midwaters will do the same as *Corynopoma* when in captivity. *Corynopoma riisei* and *Gephyrocharax atricaudatus* when kept in a tank over one meter in depth will ordinarily concentrate at about the mid-depth of the aquarium and will occur as often at the bottom as at the surface, except when fed food placed at the surface where they have been conditioned to find it.

Nelson (1964a:82) observed glandulocaudines in aquaria to feed at the surface more frequently than nonglandulocaudine characids. Many of the glandulocaudines observed in the wild (by Weitzman and Menezes) do strike and take insect prey from the water's surface, as do other midwater characid fishes with and without oblique mouths. However, in the wild, glandulocaudines were not noted to feed at the surface more often than tetragonopterine characids present. These observations are casual and no statistical evaluation is available; more critical evaluation is needed. In our view, Nelson's hypothesis that glandulocaudines are top feeders to a greater extent than tetragonopterines is doubtful. In order to more critically evaluate it, more information is needed not only on internal fertilization but also on glandulocaudine surface-feeding in the wild and on the comparative frequency of surface-feeding in various other characid subgroups. Our view does not preclude a correlation between surface-feeding and the evolution of internal fertilization in certain fishes.

Although there is a lack of evidence corroborating Nelson's hypotheses of internal fertilization and monophyly for glandulocaudines as a whole, there is also as yet a lack of evidence corroborating alternate hypotheses of relationship between any glandulocaudine subgroups and nonglandulocaudine characids. Thus we decline to discuss extensively the question of the monophyly of the Glandulocaudinae as a whole until the groups of genera now considered glandulocaudines are better studied. Preliminary investigation by the senior author indicates that the Glandulocaudinae may contain four or more monophyletic subgroups based on morphological evidence. The research presented above may be considered a first step in diagnosing one of those groups.

Despite our comments about Nelson's speculative hypotheses, we believe that he supplied a new and valuable approach to glandulocaudine research and presented morphological as well as behavioral data in far greater detail and accuracy than had been published previously. We expect Nelson's pioneering behavioral studies will prove extremely valuable for glandulocaudine phylogenetic analyses when these kinds of data become available for a wider range of glandulocaudines and other characids.

Addendum

After the above went to press we discovered a paper by E. Roloff (1949, *Microbrycon cochui* Ladiges. *Wochenschrift für Aquarien und Terrarienkunde* (Braunschweig), 43(12):337–339) providing some information on internal fertilization in *Tyttocharax cochui.* Roloff received live specimens of this species from the same source as Ladiges (1950). See page 110 above. He was successful in breeding the species and reported clear evidence of internal fertilization, although he did not see fertilization take place. On a number of occasions he removed a female that appeared ripe or showed signs of spawning to a separate tank. On at least one occasion he observed the spawning act. On other occasions he discovered only the eggs and/or young. Eggs varied greatly in number in different spawnings but were always observed on a single plant leaf; young hatched 24 hours after spawning occurred (at 23° to 25°C). Although Roloff did not report courtship behavior he did describe swimming activity, an up-and-down darting motion and vertical "standing" just below the surface of the water that might have been courtship behavior. He did not report on the length of time after separation from the male that a female produced viable eggs nor on details of egg placement on the leaf.

These observations indicating internal fertilization in a member of an additional lineage of glandulocaudines, the xenurobryconins, constitute a significant piece of evidence concerning the hypothesis of glandulocaudine monophyly.

We thank Lee A. Fuiman for providing the translation of Roloff (1949).

Literature Cited

Atkins, D.L., and W.L. Fink

1979. Morphology and Histochemistry of the Caudal Gland of *Corynopoma riisei* Gill. *Journal of Fish Biology,* 14:465–469, 1 plate.

Böhlke, J.E.

1954. Studies on Fishes of the Family Characidae, No. 7: A New Genus and Species of Glandulocaudine Characids from Central Brazil. *Stanford Ichthyological Bulletin,* 4(4):265–274.

1958a. Studies of Fishes of the Family Characidae, No. 14: A Report on Several Extensive Recent Collections from Ecuador. *Proceedings of the Academy of Natural Sciences of Philadelphia,* 110:1–121.

1958b. Results of the Catherwood Foundation Peruvian Amazonian Expedition: The Descriptions of Two New Xenurobryconine Characids. *Copeia,* 1958(4):318–325.

Breder, C. M., and D. E. Rosen

1966. *Modes of Reproduction in Fishes.* 941 pages. New York: The American Museum of Natural History.

Bussing, W.A.

1974. *Pterobrycon myrnae,* a Remarkable New Glandulocaudine Characid Fish from Costa Rica. *Revista de Biologia Tropical* (Costa Rica), 22(11):135–159.

Bussing, W.A., and T.R. Roberts

1971. Rediscovery of the Glandulocaudine Fish *Pterobrycon* and Hypothetical Significance of Its Spectacular Humeral Scales (Pisces: Characidae). *Copeia,* 1971(1):179–181.

Collette, B.B.

1977. Epidermal Breeding Tubercles and Bony Contact Organs in Fishes. *In* R.I.C. Spearman, editor, *Symposia of the Zoological Society of London,* 39:225–268. New York: Academic Press.

Cope, E.D.

1894. On Three New Species of Characinidae. *American Naturalist,* 28(325):67.

Dahl, G.

1971. *Los Peces del Norte de Colombia.* 391 pages. Bogota: Ministerio de Agricultura, Instituto de Desarollo de Recursors Naturales Renovables (INDERENA)

Eigenmann, C.H.

1910. Catalogue of the Freshwater Fishes of Tropical South Temperate America. In *Report of the Princeton University Expedition to Patagonia 1896–1899,* 3(4):375–511.

1911a. Description of Two New Tetragonopterid Fishes in the British Museum. *Annals and Magazine of Natural History,* series 8, 7:215–217.

1911b. III: New Characins in the Collections of the Carnegie Museum. *Annals of the Carnegie Museum,* 8(1):164–181.

1912. Some Results from an Ichthyological Reconnaissance of Colombia, South America. *Indiana University Studies,* 10(3):1–27.

1913. Some Results from an Ichthyological Reconaissance of Colombia, South Amercia, Part II. *Indiana Univeristy Studies,* (unnumbered volume):1–31.

1914. Some Results from Studies of South American Fishes. *Indiana University Studies,* 12(1):20–48.

1922. The Fishes of Western South America, Part I. *Memoirs of the Carnegie Museum,* 9(1):1–346, 37 plates.

1927. The American Characidae. *Memoirs of the Museum of Comparative Zoology* (Harvard College), 43(4):311–428, plates 34–39, 55, 58–60, 65, 67, 68, 75–77, 84, 86, 88, 90, 91, 96, 97, 99.

Eigenmann, C.H., A. Henn, and C. Wilson

1914. New Fishes from Western Colombia, Ecuador, and Peru. *Indiana University Studies,* 19:1–15.

Eigenmann, C.H., W.L. McAtee, and D.P. Ward

1907. On Further Collections of Fishes from Paraguay. *Annals of the Carnegie Museum,* 4(2):110–157, plates 31–45.

Eigenmann, C.H., and G.S. Myers

1929. The American Characidae, 5. *Memoirs of the Museum of Comparative Zoology* (Harvard College), 43(5):429–515 and supplement pages 516–558, plates 57, 63, 70–74, 81–83, 94.

Ellis, M.D.

1911. II: On the Species of *Hasemania, Hyphessobrycon,* and *Hemigrammus* Collected by J.D. Haseman for the Carnegie Museum. *Annals of the Carnegie Museum,* 8(1):148–163, plates 1–3.

Fernandez-Yepez, A., and J.R. Anton

1966. *Estudio (Analisis) Ictiologico "Las Majaguas", Hoyas de los Rios "Cojedes-Sarare", Edo Portuguesa.* [4] + 100 pages. Venezuela: Ministerio de Obras Publicas, Direccion de Obras Hidraulica. [In Spanish.]

Fernandez-Yepez, A., and F. Martin S.

1953. Apuntes sobre la Ictiologia de Perija. *Memoria de la Sociedad de Ciencias Naturales la Salle,* 13(35):227–243.

Fink, W.L.

1982. The Conceptual Relationships between Ontogeny and Phylogeny. *Paleobiology,* 8(3):254–264.

Fink, W.L., and S.H. Weitzman

1974. The So-called Cheirodontin Fishes of Central

America with Descriptions of Two New Species (Pisces:Characidae). *Smithsonian Contributions to Zoology,* 172: 46 pages, 26 figures.

Fowler, H.W.

1913. Fishes from the Madeira River, Brazil. *Proceedings of the Academy of Natural Sciences of Philadelphia,* 65:517–579.

1943. Zoological Results of the Second Bolivian Expedition for the Academy of Natural Sciences of Philadelphia 1936–1937, Part II: Additional New Fishes. *Notulae Naturae,* 120:1–7.

1949. Description of a New Genus and Species of Characin (*Pristicharax hanseni*) from Goiaz, Brazil. *Notulae Naturae,* 216:1–3.

1951. Os Peixes de Agua Doce do Brasil (3a entrega). *Arquivos de Zoologia do Estado do São Paulo,* 6:i–xii, 405–628.

1975a. A Catalog of World Fishes (XXII). *Quarterly Journal of the Taiwan Museum,* 28(1 and 2):1–124.

1975b. A Catalog of World Fishes (XXIII). *Quarterly Journal of the Taiwan Museum,* 28(3 and 4):278–401.

Géry, J.

1963. *Tyttocharax madeirae* and Other Xenurobryconine Characids. *Tropical Fish Hobbyist* (New Jersey), 12(2):11–15, 58, 59, 62.

1964. *Glandulocauda terofali* sp. nov., un nouveau poisson characoïde de la Republique Argentine, avec une note sur la "glande" caudal des Stevardiidi. *Opuscula Zoologica,* 78:1–12.

1965a. A New Genus from Brazil—*Brittanichthys,* a New Sexually Dimorphic Characid Genus with Peculiar Caudal Ornament, from the Rio Negro, Brazil, with a Discussion of Certain Cheirodontin Genera and a Description of Two New Species, *B. axelrodi* and *B. myersi. Tropical Fish Hobbyist* (New Jersey), 13(6):13, 14, 18, 20–24, 61–65, 67–69, figures 1–8.

1965b. Poissons Characoides Sud-americains du Senkenberg Museum, II: Characidae et Crenuchidae de l'Igarape Prêto (Haute Amazonie). [Fin]. *Senckenbergiana Biologica,* 46(3):195–218, plates 18 and 18a.

1966. A Review of Certain Tetragonopterinae (Characidae), with the Description of Two New Genera. *Ichthyologica, the Aquarium Journal* (New Jersey), 37(5):211–236.

1973. New and Little-Known Aphyoditeina (Pisces, Characoidei) from the Amazon Basin. *Studies on the Neotropical Fauna,* 8(1973):81–137.

1977. *Characoids of the World.* 672 pages. Neptune City, New Jersey: TFH Publications.

Gill, T.N.

1858. Synopsis of the Fresh Water Fishes of the Western Portion of the Island of Trinidad, W.I. *Annals of the Lyceum of Natural History* (New York), 6:363–429 [pp. 1–70 in reprint].

Günther, A.

1864. *Catalog of the Fishes in the Collection of the British Museum.* Volume 5, xii + 455 pages. London.

Hecht, M.K., and J.L. Edwards

1977. The Methodology of Phylogenetic Inference above the Species Level. *In* M.K. Hecht, P.C. Goody, and B.M. Hecht, editors, *Major Patterns in Vertebrate Evolution,* 14:3–51. New York: Plenum Press.

Hennig, W.

1966. *Phylogenetic Systematics.* 263 pages. Chicago: University of Illinois Press.

Hildebrand, S.F.

1938. A New Catalogue of the Fresh-water Fishes of Panama. *Field Museum of Natural History, Zoological Series,* 22(4):215–359.

Iwai, T.

1967. Structure and Development of Lateral Line Cupulae in Teleost Larvae. *In* P.H. Cahn, editor, *Lateral Line Detectors,* pages 27–44. Bloomington: Indiana University Press.

Kner, R.

1863. Eine Übersicht der ichthyologischen Ausbeute des Herrn Professor Dr. Mar. Wagner in Central-Amerika. *Sitzungsberichte der Akademie der Wissenschaften* (München), 2:220–230.

Kutaygill, N.

1960. Insemination, Sexual Differentiation, and Secondary Sex Characters in *Stevardia albipinnis* Gill. *Hidrobiologie, Istanbul Universitat Fen Fakultesi Mecumuasi,* series B, 24:93–128.

Ladiges, W.

1950. *Microbrycon cochui* spec. nov., eine neue Art der südamerikanischen Glandulocaudinae. *Zoologischer Anzeiger,* 145(11/12):305–309.

Leyton, L.

1975. *Fluid Behaviour in Biological Systems.* xii + 235 pages. Oxford: Clarendon Press.

Liley, N.R.

1982. Chemical Communication in Fish. *Canadian Journal of Fisheries and Aquatic Sciences,* 39(1):22–35.

Liley, N.R., and N.E. Stacey

1983. Hormones, Pheromones, and Reproductive Behavior in Fish. *In* W.S. Hoar, D.J. Randall, and E.M. Donaldson, editors, *Fish Physiology,* 9(B):1–63. New York and London: Academic Press.

Mahnert, V., and J. Géry

1984. Poissons Characoïdes (Characoidea) du Paraguay, I: *Xenurobrycon macropus* Myers et Miranda-Ribeiro. *Revue Suisse Zoologie,* 91(2):497–513.

Meek, S.E., and S.F. Hildebrand

1912. Descriptions of New Fishes from Panama. *Field Museum of Natural History, Zoological Series,* 10(6):67–68. [Publication 158]

1916. The Fishes of the Freshwaters of Panama. *Field Museum of Natural History, Zoological Series,* 10(15):217–374. [Publication 191.]

Miles, R.

1943. *Estudio Economico y Ecologico de los Peces de Agua Dulce del Valle del Cauca.* 97 pages. Secretaria de Agricultura y Fomento del Departamento Cali, Colombia.

1947. *Los Peces del Rio Magdalena.* 214 pages + 27 pages of appendices. Bogotá: Ministerio de la Economia Nacional Seccion de Piscicultura, Pesca y Caza.

Miranda-Ribeiro, A. de

1908. Peixes da Ribeira: Resultados de excursão do Sr. Ricardo Krone, membro correspondente do Museu Nacional do Rio de Janeiro. *Kosmos, Revista Artistica, Scientifica e Litteraria* (Rio de Janeiro), 5(2): 5 unnumbered pages.

1939. Alguns novos dados ictiologicos da nossa fauna. *Boletim da Biologico* (Clube Zoologico do Brasil, São Paula), new series, 4(3):358–363.

Müller, J., and F.H. Troschel

1844. Synopsis generum et specierum familiae Characinorum (Prodromus descriptionis novorum generum et specierum). *Archiv für Naturgeschichte* (Berlin), 10(1):81–99.

Myers, G.S.

1926. Eine neue Characidengattung der Unterfamilie Cheirodontinae aus Rio de Janeiro, Brasilien. *Blätter für Aquarien- und Terrarienkunde,* 37(24):1–2.

1927. Descriptions of New South American Fresh-water Fishes Collected by Dr. Carl Ternetz. *Bulletin of the Museum of Comparative Zoology* (Harvard College), 68(3):107–135.

1933. *Stevardia albipinnis? The Home Aquarium Bulletin* (East Orange, New Jersey), 3(4):11.

1934. Über den Namen des Zwergdrachenflossers, *Corynopoma riisei* Gill (= *Stevardia albipinnis* Gill). *Wochenschrift für Aquarien- und Terrarienkunde* (Braunschweig), 31(48):755–756.

1943. George S. Myers Reports. *The Aquarium* (Philadelphia), 12(6):104–106.

1953. Hints to Fish Importers . . . No. 10 (A Strange Glandulocaudine Characin from the Rio das Velhas. *The Aquarium Journal* (San Francisco), 24(6):137.

Myers, G.S., and J.E. Böhlke

1956. The Xenurobryconini, a Group of Minute South American Characid Fishes with Teeth Outside the Mouth. *Stanford Ichthyological Bulletin,* 7(2):6–12.

Myers, G.S., and P. de Miranda-Ribeiro

1945. A Remarkable New Genus of Sexually Dimorphic Characid Fishes from the Rio Paraguay Basin in Matto Grosso. *Boletim do Museu Nacional do Rio de Janeiro, Nova Serie Zoologia,* 32:1–8.

Nelson, K.

1964a. Behavior and Morphology in the Glandulocaudine Fishes (Ostariophysi, Characidae). *University of California Publications in Zoology,* 75(2):59–152.

1964b. The Temporal Patterning of Courtship Behavior in the Glandulocaudine Fishes (Ostariophysi, Characidae). *Behaviour,* 14(1–2):90–146.

1964c. The Evolution of a Pattern of Sound Production Associated with Courtship in the Characid Fish, *Glandulocauda inequalis. Evolution,* 18(4):526–540.

Nichols, J.T.

1913. On Two New Characins in the American Museum. *Proceedings of the Biological Society of Washington,* 26:151–152.

Patterson, C.

1982. Morphological Characters and Homology. In K.A. Joysey and A.E. Friday, editors, *Problems of Phylogenetic Reconstruction,* pages 21–74. London and New York: Academic Press.

Pearson, N.E.

1924. The Fishes of the Eastern Slope of the Andes, 1: The Fishes of the Rio Beni Basin, Bolivia, Collected by the Mulford Expedition. *Indiana University Studies,* 11(64):1–83.

Perugia, A.

1891. Appunti sopra alcuni Pesci Sud-Americani Conservati nel Museo Civico di Storia Naturale di Genova. *Annali del Museo di Storia Naturale di Genova,* series 2, 10(30):603–657.

Platnick, N.I., and G. Nelson

1978. A Method of Analysis for Historical Biogeography. *Systemic Zoology,* 27(1):1–16.

Ramirez, M.V.

1960. Nuevos Peces para la Fauna Venezolana. *Memorias de la Sociedad de Ciencias Naturales "La Salle"* (Caracas), 20:126–131.

Regan, C.T.

1907. Description of Two New Characinid Fishes from South America. *Annals and Magazine of Natural History,* series 7, 20:402–403.

1913. The Fishes of the San Juan River, Colombia. *Annals and Magazine of Natural History,* series 8, 12:462–473.

Reinhardt, J.

1866. Om trende, formeentligt ubeskrevne Fisk af Characinernes eller Karpelexenes Familie. *Oversigt over det danske Videnskabernes Selskals Forhandlinger og dets Medlemmers Arbeider i Aaret* (Kjöbenhavn), pages 49–68, plates 1, 2.

Roberts, T.R.

1970. Scale-Eating American Characoid Fishes, with Special Reference to *Probolodus heterostomus. Proceedings of the California Academy of Sciences,* fourth series, 38(20):383–390.

1973. The Glandulocaudine Characid Fishes of the Guayas Basin in Western Ecuador. *Bulletin of the Museum of Comparative Zoology* (Harvard University), 144(8):489–514, figures 1–26.

Rosen, D.E.

1978. Vicariant Patterns and Historical Explanation in Biogeography. *Systematic Zoology,* 27(2):159–188.

Schultz, L.P.

1944. The Fishes of the Family Characinidae from Venezuela, with Descriptions of Seventeen New Forms. *Proceedings of the United States National Museum,* 95(3181):235–367.

1959. The Generic Status of *Mimagoniates* and *Glandulocauda,* South American Characid Fishes. *Tropical Fish Hobbyist* (New Jersey), 8(2):6–11, 63–64.

Sober, E.

In press. Parsimony and Character Weighting. *Cladistics.*

Steindachner, F.

1876. Ichthyological Beitrage (V.), II: Über einige neue Fischarten, insbesondere Characinen und Siluroiden aus dem Amazonenstrome. *Sitzungsberichte der Akademie der Wissenschaften* (Wien), 74:73–176.

Tortonese, E.

1941–1942. Ricerche ed Osservazioni sui Caracidi delle Sottofamiglie Tetragonopterinae, Glandulocaudinae e Stethaprioninae (Teleostei Plectospondyli). *Bollettino dei Musei di Zoologia ed Anatomia Comparata della Reale Università di Torino,* series 4, 117:11–86.

Travassos, H.

1951. Catalogo dos Gêneros e Subgêneros da Subordem Characoidei (Actinopterygii). *Dusenia* (Curitiba, Brazil), 2(3):205–244. [pp. 1–20 of separate.]

1952. Catalogo dos Gêneros e Subgêneros da Subordem Characoidei (Actinopterygii). *Dusenia* (Curitiba, Brazil), 3(3):225–250, [pp. 117–142 of separate.]

Vari, R.P.

1982. Systematics of the Neotropical Characoid Genus *Curimatopsis* (Pisces: Characoidei). *Smithsonian Contributions to Zoology,* 373: 28 pages, 21 figures.

Weitzman, S.H.

1954. The Osteology and the Relationships of the South American Characid Fishes of the Subfamily Gasteropelecinae. *Stanford Ichthyological Bulletin,* 4(4):213–263, figures 1–18.

1962. The Osteology of *Brycon meeki,* a Generalized Characid Fish, with an Osteological Definition of the Family. *Stanford Ichthyological Bulletin,* 8(1):1–77.

1975. Der Flügelschuppensalmer, *Pterobrycon myrnae,* ein bezaubernder Aquarienfisch der Zukunft aus Costa Rica. *Die Aquarien- und Terrarien-Zeitschrift,* 28(12):[406–410], 5 unnumbered figures.

1982. Glandulocaudine Characids and Putative Pheromone Pumps [Abstract]. *The 62nd Annual Meeting of the American Society of Ichthyologists and Herpetologists, Program and Abstracts* (Northern Illinois University), 1 unnumbered page.

1985. Biogeography of the Glandulocaudine Characid Freshwater Fishes of South America. In *National Geographic Society Research Reports, 1977 Projects,* 18:775–778. Washington, D.C.: National Geographic Society.

Weitzman, S.H., and C.A.G. da Cruz

1981. The South American Fish Genus *Rachoviscus,* with a Description of a New Species (Teleostei: Characidae). *Proceedings of the Biological Society of Washington,* 93(4):997–1015.

Weitzman, S.H., and W.L. Fink

1983. Relationships of the Neon Tetras, a Group of South American Freshwater Fishes (Teleostei, Characidae) with Comments on the Phylogeny of the New World Characiforms. *Bulletin of the Museum of Comparative Zoology* (Harvard University), 150(6):339–395, figures 1–30.

Weitzman, S.H., and J. Géry

1981. The Relationships of the South American Pygmy Characoid Fishes of the Genus *Elachocharax,* with a Redescription of *Elachocharax junki* (Teleostei: Characidae). *Proceedings of the Biological Society of Washington,* 93(4):887–913.

Weitzman, S.H., and R.H. Kanazawa

1977. A New Species of Pygmy Characoid Fish from the Rio Negro and Rio Amazonas, South America (Teleostei: Characidae). *Proceedings of the Biological Society of Washington,* 90(1): 149–160.

Weitzman, S.H., and J.E. Thomerson

1970. A New Species of Glandulocaudine Characid Fish, *Hysteronotus myersi* from Peru. *Proceedings of the California Academy of Sciences,* fourth series, 38(8):139–156.

Weitzman, S.H., and M. Weitzman

1982. Biogeography and Evolutionary Diversification in Neotropical Freshwater Fishes, with Comments on the Refuge Theory. *In* G.T. Prance, editor, *Biological Diversification in the Tropics,* pages 403–422. New York: Columbia University Press.

Wiley, E.O.

1981. *Phylogenetics, the Theory and Practice of Phylogenetic Systematics.* 439 pages, New York: John Wiley and Sons.

Wiley, M.L., and B.B. Collette

1970. Breeding Tubercles and Contact Organs in Fishes: Their Occurrence, Structure, and Significance. *Bulletin of the American Museum of Natural History,* 143(3):143–216.

REQUIREMENTS FOR SMITHSONIAN SERIES PUBLICATION

Manuscripts intended for series publication receive substantive review within their originating Smithsonian museums or offices and are submitted to the Smithsonian Institution Press with Form SI-36, which must show the approval of the appropriate authority designated by the sponsoring organizational unit. Requests for special treatment—use of color, foldouts, casebound covers, etc.—require, on the same form, the added approval of the sponsoring authority.

Review of manuscripts and art by the Press for requirements of series format and style, completeness and clarity of copy, and arrangement of all material, as outlined below, will govern, within the judgment of the Press, acceptance or rejection of manuscripts and art.

Copy must be prepared on typewriter or word processor, double-spaced, on one side of standard white bond paper (not erasable), with 1¼" margins, submitted as ribbon copy (not carbon or xerox), in loose sheets (not stapled or bound), and accompanied by original art. Minimum acceptable length is 30 pages.

Front matter (preceding the text) should include: **title page** with only title and author and no other information; **abstract** page with author, title, series, etc., following the established format; table of **contents** with indents reflecting the hierarchy of heads in the paper; also, **foreword** and/or **preface**, if appropriate.

First page of text should carry the title and author at the top of the page; **second page** should have only the author's name and professional mailing address, to be used as an unnumbered footnote on the first page of printed text.

Center heads of whatever level should be typed with initial caps of major words, with extra space above and below the head, but with no other preparation (such as all caps or underline, except for the underline necessary for generic and specific epithets). Run-in paragraph heads should use period/dashes or colons as necessary.

Tabulations within text (lists of data, often in parallel columns) can be typed on the text page where they occur, but they should not contain rules or numbered table captions.

Formal tables (numbered, with captions, boxheads, stubs, rules) should be submitted as carefully typed, double-spaced copy separate from the text; they will be typeset unless otherwise requested. If camera-copy use is anticipated, do not draw rules on manuscript copy.

Taxonomic keys in natural history papers should use the aligned-couplet form for zoology and may use the multi-level indent form for botany. If cross referencing is required between key and text, do not include page references within the key, but number the keyed-out taxa, using the same numbers with their corresponding heads in the text.

Synonymy in zoology must use the short form (taxon, author, year:page), with full reference at the end of the paper under "Literature Cited." For botany, the long form (taxon, author, abbreviated journal or book title, volume, page, year, with no reference in "Literature Cited") is optional.

Text-reference system (author, year:page used within the text, with full citation in "Literature Cited" at the end of the text) must be used in place of bibliographic footnotes in all Contributions Series and is strongly recommended in the Studies Series: "(Jones, 1910:122)" or ". . . Jones (1910:122)." If bibliographic footnotes are required, use the short form (author, brief title, page) with the full citation in the bibliography.

Footnotes, when few in number, whether annotative or bibliographic, should be typed on separate sheets and inserted immediately after the text pages on which the references occur. Extensive notes must be gathered together and placed at the end of the text in a notes section.

Bibliography, depending upon use, is termed "Literature Cited," "References," or "Bibliography." Spell out titles of books, articles, journals, and monographic series. For book and article titles use sentence-style capitalization according to the rules of the language employed (exception: capitalize all major words in English). For journal and series titles, capitalize the initial word and all subsequent words except articles, conjunctions, and prepositions. Transliterate languages that use a non-Roman alphabet according to the Library of Congress system. Underline (for italics) titles of journals and series and titles of books that are not part of a series. Use the parentheses/colon system for volume(number):pagination: "10(2):5–9." For alignment and arrangement of elements, follow the format of recent publications in the series for which the manuscript is intended. Guidelines for preparing bibliography may be secured from Series Section, SI Press.

Legends for illustrations must be submitted at the end of the manuscript, with as many legends typed, double-spaced, to a page as convenient.

Illustrations must be submitted as original art (not copies) accompanying, but separate from, the manuscript. Guidelines for preparing art may be secured from Series Section, SI Press. All types of illustrations (photographs, line drawings, maps, etc.) may be intermixed throughout the printed text. They should be termed **Figures** and should be numbered consecutively as they will appear in the monograph. If several illustrations are treated as components of a single composite figure, they should be designated by lowercase italic letters on the illustration; also, in the legend and in text references the italic letters (underlined in copy) should be used: "Figure 9b." Illustrations that are intended to follow the printed text may be termed **Plates**, and any components should be similarly lettered and referenced: "Plate 9b." Keys to any symbols within an illustration should appear on the art rather than in the legend.

Some points of style: Do not use periods after such abbreviations as "mm, ft, USNM, NNE." Spell out numbers "one" through "nine" in expository text, but use digits in all other cases if possible. Use of the metric system of measurement is preferable; where use of the English system is unavoidable, supply metric equivalents in parentheses. Use the decimal system for precise measurements and relationships, common fractions for approximations. Use day/month/year sequence for dates: "9 April 1976." For months in tabular listings or data sections, use three-letter abbreviations with no periods: "Jan, Mar, Jun," etc. Omit space between initials of a personal name: "J.B. Jones."

Arrange and paginate sequentially every sheet of manuscript in the following order: (1) title page, (2) abstract, (3) contents, (4) foreword and/or preface, (5) text, (6) appendixes, (7) notes section, (8) glossary, (9) bibliography, (10) legends, (11) tables. Index copy may be submitted at page proof stage, but plans for an index should be indicated when manuscript is submitted.