# A PHYLOGENETIC AND BIOGEOGRAPHIC ANALYSIS OF CYPRINODONTIFORM FISHES (TELEOSTEI, ATHERINOMORPHA)

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# ABSTRACT

The cyprinodontiforms, or killifishes, are a large and diverse group of 900 fresh- and brackish-water species with a pantropical and temperate Laurasian distribution. Traditionally, it has been classified in five families: the worldwide, oviparous Cyprinodontidae, and four New World viviparous families: the Poeciliidae, Anablepidae, Jenynsiidae, and Goodeidae. Fishes of the diverse Cyprinodontidae, in turn, have been divided into as many as eight subfamilies.

The objectives of the present study are to: (1) determine if the cyprinodontiform fishes as a whole form a monophyletic group; (2) determine if each of the five families is monophyletic; (3) define the major subgroups of cyprinodontiforms, concentrating on the genera of the Cyprinodontidae; (4) determine the interrelationships of the subgroups; (5) present a comprehensive classification of the cyprinodontiforms that reflects the interrelationships; and (6) provide a hypothesis for the distribution of the group.

The following general results were obtained by using the methods of phylogenetic systematics and vicariance biogeography: (1) the cyprinodontiforms are considered to be monophyletic by their sharing derived characters of the caudal skeleton, upper jaw, gill arches, position of the first pleural rib, pectoral girdle, and aspects of breeding and development; (2) the family Cyprinodontidae is nonmonophyletic as it contains some of the most primitive and derived cyprinodontiforms; (3) each of the four viviparous families is monophyletic; however, their previous definitions in terms of uniquely derived characters have been altered; (4) the development of an annual habit, exhibited by members of the aplocheiloid killifishes and possibly some cyprinodontoids, includes derived reproductive traits exhibited to some degree by all killifishes; therefore, the annual habit does not define a monophyletic group of killifishes; (5) similarly, viviparity is not hypothesized to be a uniquely derived character, but has apparently arisen at least three times within the group; and (6) the interrelationships of cyprinodontiforms correspond, in part, with a pattern of the break-up of Pangea, except for an Andean-Eurasian sister group pair.

A scheme of interrelationships of cyprinodontiforms as well as of monophyletic subgroups is presented in the form of cladograms, of which the former is transformed into a comprehensive classification of the group. The fishes under study are recognized as comprising the order Cyprinodontiformes Berg and divided into two suborders, the Aplocheiloidei (which previously comprised, in part, the Cyprinodontidae), and the Cyprinodontoidei (comprising all other cyprinodontiforms as well as the four viviparous families). In order to minimize the number of named empty categories, a numbering system is incorporated into a traditional naming system to create the new classification.

# INTRODUCTION

The cyprinodontiforms, commonly known as killifishes, topminnows, or toothcarps, are a large and diverse group of teleostean fishes distributed nearly worldwide in temperate and tropical freshwaters (fig. 1), with some members regularly entering brackish water.

The term cyprinodontiforms as used in this paper refers to fishes of the five families of the superfamily Cyprinodontoidea, order Atheriniformes (Rosen, 1964). These are the cosmopolitan and oviparous Cyprinodontidae, and four New World viviparous families, the Anablepidae, Goodeidae, Jenynsiidae, and Poeciliidae.

The Cyprinodontidae are the largest and most diverse family containing over 650 nominal species in approximately 80 nominal genera. Included are the popular aquarium fishes, including the annual killifishes of tropical South America and Africa of the subfamily Rivulinae (Myers, 1955), and widely used experimental fish such as those of the genus *Fundulus*.

Of the four viviparous families, two, the Mexican, Central American, and northern South American Anablepidae, and the southeastern South American Jenynsiidae, contain just one genus each with several species. The Goodeidae are diverse, comprising approximately 35 species in 16 genera, all of which are restricted to the Mexican Plateau (Miller and Fitzsimons, 1971). The Neotrop-

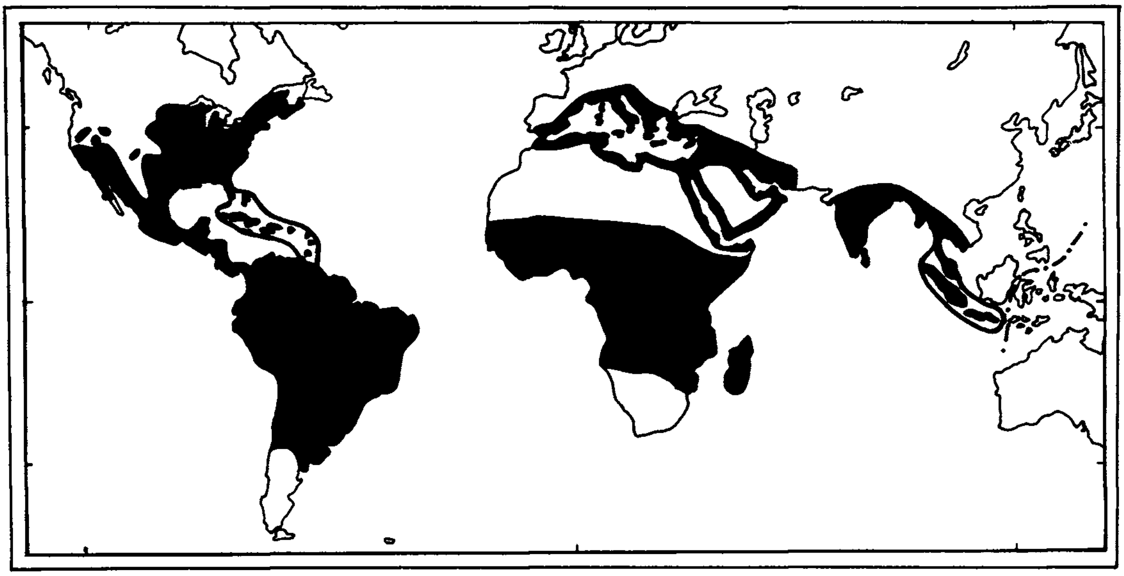

FIG. 1. Present day distribution of cyprinodontiforms. Dotted and dashed line approximates Wallace's Line.

ical and temperate Poeciliidae comprise approximately 200 species in 19 genera (Rosen and Bailey, 1963; Rosen, 1979), and the guppy (*Poecilia reticulata*) and mosquito-fish (*Gambusia affinis*) are included.

Knowledge of the relationships of the cyprinodontiforms to other fishes has advanced considerably, whereas the proposed interrelationships of cyprinodontiforms has progressed little since Garman's (1895) outline of the major subgroups.

Killifishes are typically soft-rayed, and, as such, have historically been aligned with the more primitive teleost groups. Gill (1874) aligned the cyprinodontiforms with the esocoids, which together comprised the order Haplomi. Starks (1904) divided the Haplomi into three suborders: the Esocoidei (including the mud-minnow *Umbra*, and the pike *Esox*), the Amblyopsioidei (the cavefishes), and the Poecilioidei (=Cyprinodontoidei of Rosen, 1964). Yet, he admitted there were no important [unique] characters which defined the order.

Regan (1911) remarked on the killifish and cavefish relationship to more derived teleost groups while noting that the esocoids were relatively primitive. He included as evidence for this distinction the fact that in esocoids the maxilla enters the gape, whereas the maxilla is excluded from the gape in killifishes (including the adrianichthyoids) and cavefishes. Regan (1909) separated the last two groups from the rest of the Haplomi and constructed for them a new order Microcyprini.

This action was supported by Hubbs (1919) who reported that the Microcyprini (including the phallostethoids after Regan, 1913) have a derived branchiostegal number and arrangement, comparable to those of the acanthopterygians; whereas, the Haplomi, *sensu* Regan, are primitive in this regard.

Myers (1928a) removed the phallostethoid fishes from the Microcyprini, and suggested their close relationship to the Atherinidae, then in the order Percesoces.

The alignment of the amblyopsoids with the cyprinodontiforms and adrianichthyoids was never more than tentative; yet it remained unchallenged until Rosen (1962) removed the cavefishes from the Microcyprini, referred to as the Cyprinodontiformes following Berg (1940), and placed them in the newly created Amblyopsiformes which he claimed was more closely related to the Percopsiformes. The cyprinodontiforms and adrianichthyoids remained as the sole constituents of the order Cyprinodontiformes.

Gosline (1963) continued to support the naturalness of the order Microcyprini, and criticized Rosen (1962) for separating the order into two groups while giving no hint as to the placement of the Cyprinodontiformes in a higher classification of teleost fishes.

An answer to this was provided by Rosen (1964) when he created the order Atheriniformes to include the cyprinodontiforms, adrianichthyoids, atherinoids, phallostethoids, exocoetoids, and scomberesocoids. Rosen's (1964) classification is summarized in table 1.

The alignment of these fishes had casually been suggested earlier by several workers, although, this was done with little formal taxonomic treatment. Cope (1870) first remarked on the possible close relationship of atherinids and cyprinodonts. In addition, Myers (1928a) commented that the structure of the ethmoid region and the mouth suggested the affinity of cyprinodontiforms and members of the Percesoces. Furthermore, Regan (1911, p. 321), commenting on the possible alignment of his new order, said: "Whereas the Haplomi show relationship to the most generalized isospondylous fishes, the Microcyprini bear more resemblance to the Salmopercae and Synentognathi, especially the latter."

The monophyly (in the sense of Hennig, 1966) of the order Atheriniformes, and the monophyly and interrelationships of its subgroups were not rigorously defined by Rosen (1964). However, recent evidence indicates that the Atheriniformes is monophyletic, and problems of its higher order interrelationships may easily be summarized (Rosen and Parenti, MS).

Rosen (1964, p. 260) suggested that the atherinomorph fishes: "arose from a group that stood somewhere in the ancestry of the order Perciformes." This point, which may be restated as fishes of the Atherinomorpha and Percomorpha share a common ancestor, was reiterated in the classifications of Greenwood, Rosen, Weitzman and Myers (1966), Rosen and Patterson (1969), Rosen (1973a), Patterson and Rosen (1977) and Rosen and Parenti (MS), and is supported by derived features of the gill arches and the jaws and jaw suspensorium.

TABLE 1
**Classification of Fishes of the Order Atheriniformes**
(Rosen, 1964)

- Superorder Acanthopterygii
  - Series Atherinomorpha
    - Order Atheriniformes
      - Suborder Atherinoidei
        - Superfamily Atherinoidea
        - Superfamily Phallostethoidea
      - Suborder Cyprinodontoidei
        - Superfamily Adrianichthyoidea
        - Superfamily Cyprinodontoidea
          - Family Cyprinodontidae
          - Family Anablepidae
          - Family Jenynsiidae
          - Family Goodeidae
          - Family Poeciliidae
      - Suborder Exocoetoidei
        - Superfamily Exocoetoidea
        - Superfamily Scomberesocoidea
  - Series Percomorpha

Thus, with increased knowledge of interrelationships of teleosts, cyprinodontiforms have progressed from a primary alignment with the primitive esocoids to a hypothesized close relationship with the advanced percomorph fishes.

Yet, as stated previously, our knowledge of the interrelationships of members of the superfamily Cyprinodontoidea has undergone little comparable progress. Relationships among the families and among the included genera, have been presented as speculation. Workers have either dealt with the primary groups of oviparous cyprinodontiforms alone (e.g., Myers, 1931, 1955; Sethi, 1960; Uyeno and Miller, 1962), or one of the four viviparous families (e.g., Rosen and Bailey, 1963; Hubbs and Turner, 1939; Miller, 1979), never more than casually discussing the relationship of one family to another or to a group of oviparous cyprinodontids.

However, aside from discussions and repeated speculation on the affinity of one group of killifishes to another, there has been no formal treatment of the interrelationships of the five families, no statement supporting or refuting the monophyly of each of the five families, and no formal definition of the superfamily Cyprinodontoidea.

Knowledge of such interrelationships could serve as a basis for biogeographic hypotheses concerning the history of the pantropical and temperate Laurasian regions, could be an invaluable reference for research scientists and aquarists alike, and form the framework for an understanding of the variety of reproductive modes found within the group.

Thus, the objectives of this study are to: (1) determine the monophyly of the superfamily Cyprinodontoidea; (2) determine the monophyly of each of the five families; (3) define the major subgroups of cyprinodontiforms, with a concentration on the genera of the family Cyprinodontidae; (4) determine the interrelationships of the subgroups; (5) present a comprehensive classification of the cyprinodontiforms which reflects the interrelationships; and (6) provide a hypothesis for the distribution of the group.

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Vernacular Names: In a systematic study that ends with a reclassification, names must be used in the discussion of interrelationships and character distributions which are at once familiar to most workers on the group, and which unambiguously refer to a given group of genera or families. Thus, I use the following vernacular names throughout the text.

The term acanthopterygian refers to fishes of the superorder Acanthopterygii, which includes the two series Atherinomorpha and Percomorpha (Rosen, 1973a). The series are termed atherinomorph and percomorph, respectively.

The series Atherinomorpha contains a sole order, the Atheriniformes. Thus, the two categories are equivalent, and the term atherinomorph describes the membership of both. Atheriniform is therefore not used herein to avoid confusion.

Within the order Atheriniformes, vernacular names are used for the major subdivisions listed in the classification of table 1.

Fishes of the suborder Atherinoidei are referred to as the silversides. The terms atherinoid and phallostethoid are reserved for members of the superfamilies Atherinoidea and Phallostethoidea, respectively.

There is no vernacular reference for the suborder Cyprinodontoidei of Rosen; components are referred to separately. The term adrianichthyoid refers to fishes of the superfamily Adrianichthyoidea. The fishes of the superfamily Cyprinodontoidea, the subject of this revision, are referred to alternately as the cyprinodontiforms, cyprinodonts, or killifishes. They are reclassified in this study as the order Cyprinodontiformes. Two suborders are named, the Aplocheiloidei, comprising those fishes of the Rivulinae, and the Cyprinodontoidei, comprising all other cyprinodontiforms. These groups will be referred to as the aplocheiloids and cyprinodontoids, respectively.

There is no vernacular reference for the suborder Exocoetoidei, and its two superfamilies are referred to as the exocoetoids (superfamily Exocoetoidea) and the scomberesocoids (superfamily Scomberesocoidea).

Within the Cyprinodontoidea, members of the five families are normally referred to as the cyprinodontid, anablepid, jenynsiid, goodeid or poeciliid fishes. The Cyprinodontidae are also referenced as the oviparous killifishes, whereas the four remaining families are collectively referred to as the viviparous killifishes.

TABLE 2

**Current Comprehensive Classification of the Cyprinodontid Fishes**

Family Cyprinodontidae
  Subfamily Fundulinae
    Genus *Fundulus, Lucania, Leptolucania, Oxyzygonectes, Cubanichthys, Chriopeoides, Valencia, Empetrichthys, Crenichthys, Profundulus, Hubbsichthys,*[a] *Adinia*
  Subfamily Cyprinodontinae
    Genus *Cyprinodon, Megupsilon, Floridichthys, Jordanella, Cualac, Aphanius, Tellia, Kosswigichthys, Anatolichthys*
  Subfamily Lamprichthyinae
    Genus *Lamprichthys*
  Subfamily Orestiatinae
    Genus *Orestias*
  Subfamily Pantanodontinae
    Genus *Pantanodon*
  Subfamily Procatopodinae
    Genus *Aplocheilichthys, Procatopus, Hypsopanchax, Micropanchax, Cynopanchax, Plataplochilus, Platypanchax, Hylopanchax, Congopanchax, Poropanchax*
  Subfamily Rivulinae
    Genus *Rivulus, Trigonectes, Rivulichthys, Pterolebias, Rachovia, Austrofundulus, Terranotus, Cynolebias, Cynopoecilus, Campellolebias, Simpsonichthys, Aphyosemion, Nothobranchius, Adamas, Epiplatys, Aplocheilus, Pachypanchax, Fundulosoma, Callopanchax*
  Subfamily Fluviphylacinae
    Genus *Fluviphylax*

[a] Schultz (1949) described *Hubbsichthys laurae*, new genus and species of cyprinodontid. The holotype (USNM 120999), the only recorded specimen, was examined and determined as a female poeciliid, and most likely of the species *Poecilia caucana* (Steindachner). I propose *Hubbsichthys* be dropped from the subfamily and placed in synonymy of the genus *Poecilia*.

Vernacular names for the various groups found within the Cyprinodontidae follow the current classification of the family, listed in table 2.

The subfamily Cyprinodontinae is referred to as the cyprinodontines, which are further divided into the New World cyprinodontines, comprising *Cyprinodon* and its immediate relatives, and the Anatolian or Old World cyprinodontines, comprising *Aphanius* and its immediate relatives.

The subfamilies Fluviphylacinae, Orestiatinae, and Pantanodontinae are referred to as the genera *Fluviphylax, Orestias,* and *Pantanodon,* respectively. The Procatopodinae and Lamprichthyinae are collectively referred to as the procatopines.

Members of the subfamily Fundulinae, which are no longer considered to be members of a monophyletic group containing *Fundulus,* are referred to by their formal generic names (e.g., *Oxyzygonectes, Cubanichthys, Chriopeoides, Empetrichthys, Crenichthys,* and *Profundulus*). The term funduline refers to *Fundulus, Adinia, Leptolucania, Lucania* and their nominal subgenera.

Various other groups of teleosts are discussed using conventional terminology.

# METHODS

## PHYLOGENETIC ANALYSIS

The method of phylogenetic analysis adopted here is that put forth formally by Hennig (1950, 1966), alternately referred to as cladistics, cladism, or phylogenetic systematics. Within a cladistic scheme, taxa are grouped hierarchically on the basis of their sharing derived characters (termed synapomorphies), rather than on their overall similarity. This method of analysis is preferred over those of evolutionary taxonomy (e.g., Mayr, 1969, 1974; Simpson, 1961) and phenetics (e.g., Sokal and Sneath, 1963; Sneath and Sokal, 1973) if the goal is the hierarchical grouping of taxa based solely on a hypothesis of common ancestry. Given the assumption that nature is structured hierarchically, a cladogram that reflects increasing levels of generality of character distributions is concluded to be the best estimate of the one, true phylogeny.

Recognized taxa are those which can be defined as monophyletic groups in the sense of Hennig. That is, a monophyletic group contains all the descendants, and only the descendants of a common ancestor. Monophyletic groups, therefore, are defined by their members sharing derived characters. Such groups are assembled into more inclusive monophyletic groups until a hierarchical arrangement of all the members is achieved.

It is not the intention of a cladistic analysis to recognize paraphyletic groups. However, since this study is done primarily at the generic level, genera that are not monophyletic may have groups of species assignable to other monophyletic groups, leaving the remainder as a paraphyletic assemblage at the most plesiomorph position of the more inclusive monophyletic group. In these cases, the traditional generic name will be retained, and recommendations for a species-level revision will be made.

When character conflicts occur at any level in the analysis, the principle of parsimony is invoked to choose among alternative explanations of the data. The assumption is not made that evolution always, or ever, must proceed along a parsimonious course; however, it is concluded that our explanation of a hypothesized phylogeny should be the most parsimonious one since, by definition, it is the one which requires that we invoke the fewest assumptions about character transformations. Similarly, characters are not weighted in the analysis since no objective criteria for weighting could be determined.

Character transformation series are constructed among states of homologous characters. Characters are hypothesized to be homologous if they are comparable in shape and position, or present in different forms, but exhibiting the same ontogenetic sequence. A homology, therefore, is, at one level, comparable to a derived character or apomorphy (Wiley, 1975).

The polarity of a transformation series is initially determined by comparison to an outgroup (as discussed by Lundberg, 1972), or by comparison with an ontogenetic transformation (as discussed in Nelson, 1973).

In the latter procedure, an ontogenetic change in one of two taxa that are hypothesized to share a common ancestor, hence termed sister groups, must logically be considered derived if the principle of parsimony is applied. That is, one need only make the assumption that the transformation was gained by one taxon, rather than the assumptions that the character was present in the common ancestor, and that it was subsequently lost in the other.

In the former procedure, a character state is analyzed as being primitive or derived by comparing it to the state within other groups of atherinomorph fishes, within the percomorphs, or to the teleosts as a whole. Characters or character complexes recognized at once as being unique are analyzed as derived. The general state of a character in an outgroup or in the cyprinodontiforms is initially assessed as primitive. However, a character which may be described in the same manner as that of the general state may be termed secondarily derived within a group of cyprinodontiforms if this interpretation is consistent with the most parsimonious interpretation of all the data. That is, the polarity of a transformation series is not always determined by the constraint that the general state represents the primitive condition. Transformation series treated in this manner are discussed in detail.

BIOGEOGRAPHIC ANALYSIS: A hypothesis of the historical distribution of cyprinodontiform fishes is constructed upon completion of the phylogenetic analysis. The distribution of monophyletic groups should reflect the history of the areas of distribution if we accept the premise inherent in the works of Croizat (1958, 1964) that the world and its biota evolved together. This concept forms the basis of vicariance biogeography as put forth by Croizat, and Croizat, Nelson and Rosen (1974), Platnick and Nelson (1978) and Rosen (1976, 1978).

The cladogram of cyprinodontiforms may readily be transformed into a cladogram of areas occupied by monophyletic groups (Rosen, 1978). A pattern of earth history is suggested by the interrelationships of the areas. The generality of this pattern and those of monophyletic groups will be tested by comparison to other established patterns as well as to each other.

DISPOSITION OF SPECIMENS AND COLLECTION OF DATA: Counterstained specimens of cyprinodontiforms were prepared according to the alcian blue-alizarin Red S method of Dingerkus and Uhler (1977) to facilitate the examination of cartilage as well as bone. When possible, at least two males and two females of several species in a genus were prepared. In some cases, just one pair was prepared. When lots were only large enough for the preparation of one specimen a male was chosen since cyprinodontiforms are markedly sexually dimorphic with males typically exhibiting a greater degree of variation than females.

Additional specimens, which were cleared and solely alizarin-stained, were available from the collection of fishes in the Department of Ichthyology, AMNH.

Radiographs were prepared primarily of species represented only by the type material in order to facilitate a cursory examination of the osteological details.

Anatomical illustrations were prepared from sketches of structures as viewed through a camera lucida mounted on a dissecting microscope. Primarily, dissected cleared and stained material was used for this purpose; however, alcohol specimens were partially dissected when necessary. Most illustrations and descriptions of states of cartilaginous elements are of counterstained preparations.

Developmental series of available aquarium representatives of several genera of atherinomorphs were bred and reared in the vivarium of the Department of Ichthyology, AMNH. Details of development, including structure of the egg, period of time from spawning to hatching, and age at first spawning were observed for several genera. Adults were also observed for details of reproductive behavior. All preserved aquarium specimens were catalogued in the department's collection.

Measurements and counts were made according to the procedure outlined by Miller (1948) for cyprinodont fishes, except as noted. As Miller pointed out, killifishes do not possess a complete lateral line; therefore, it is customary to count scales in a lateral series starting from the shoulder girdle to the end of the hypural plate, ascertained by bending the caudal fin.

Names for skeletal structures are those traditionally used in a description of teleost anatomy, as updated by Patterson (1975). Details of the gonopodium of poeciliid fishes are described using the terminology of Rosen and Bailey (1963).

Patterns of head scales and sensory pores and canals are described according to the conventions established by Hoedeman (1958) and Gosline (1949), respectively, to facilitate comparisons among the results of this and other studies.

Estimates of number of species in groups currently classified in the Cyprinodontidae are from Lazara (1979) unless otherwise stated.

Specimens examined and their catalog numbers appear in the systematic section following each generic and family diagnosis. Catalog numbers followed by an asterisk (*) indicate lots from which counterstained specimens were prepared; those followed by a cross (+) are lots from which solely alizarin-stained preparations had been made. The number of such specimens prepared is given in both cases as a fraction of the total specimens in the lot (e.g., 4 out of 20 is given as 4/20). Catalog numbers with no designation are of alcohol lots from which no special preparations were made.

## ABBREVIATIONS

### INSTITUTIONAL

AMNH, American Museum of Natural History, New York
ANSP, Academy of Natural Sciences, Philadelphia
BMNH, British Museum (Natural History), London
CAS, California Academy of Sciences, San Francisco
FMNH, Field Museum of Natural History, Chicago
IU, Indiana University (now at California Academy of Sciences, San Francisco)
MCSN, Museo Civico di Storia Naturale, Genova
MCZ, Museum of Comparative Zoology, Cambridge
MNHN, Museum National d'Histoire Naturelle, Paris
SU, Stanford University (now at California Academy of Sciences, San Francisco)
UMMZ, University of Michigan, Museum of Zoology, Ann Arbor
USNM, National Museum of Natural History, Washington, D.C.
ZVC, Zoologia Vertebrados, de la Facultad Ciencias, Montevideo, Uruguay

### ANATOMICAL

AC, anterior ceratohyal
ALV, alveolar arm of premaxilla
AMR, middle anal radial
APL, autopalatine
APR, proximal anal radial
AR 1, anal ray 1
ART, articular
ASC, ascending process of premaxilla
BOC, basioccipital
BR, branchiostegal ray
CL, cleithrum
COR, coracoid
DEN, dentary
DHH, dorsal hypohyal
DMX, dorsal process of maxilla
DPR, proximal dorsal radial
DR1, first dorsal ray
E 1–4, epibranchial 1–4
END, endopterygoid
EP, epural
EPL, epipleural rib
EPO, epiotic
EPO-PRO, epiotic processes
EXO, exoccipital
FRO, frontal
HY 1–5, hypural 1–5
HYO, hyomandibula
HYP, hypaxial musculature
ICARM, infracarnalis medius
ICARP, infracarnalis posterior
IF, inferior pharyngeals
IH, interhyal
INCLA, inclinatores anales
IS, ischial process

K, kidney
MAX, maxilla
MDN, medial process of dentary
MET, metapterygoid
NA-1, neural arch 1
NL, nasal
NS, neural spine
PAR, parietal
PAS, parasphenoid
PB 1–3, pharyngobranchial 1–3
PC, posterior ceratohyal
PCL1, 3, postcleithrum 1, 3
PHY, parhypural
PL, pleural rib
PMX, premaxilla
POP, preopercle
PRO, prootic
PSP, pseudophallus
PTT, posttemporal
PU2, preural centrum 2
QUA, quadrate
RAD, radials
RC, rostral cartilage
RET, retroarticular
SAC, subautopalatine cartilage
SCL, supracleithrum
SOC, supraoccipital
SOC-PRO, supraoccipital processes
SPH, sphenotic
SYM, symplectic
T, testis
TPB 1–4, pharyngobranchial toothplate 1–4
UB, urinary bladder
UG, urogenital opening
UN, uroneural
UR, ureter
VHH, ventral hypohyal
VMX, ventral process of maxilla
VO, vomer

## OVERVIEW OF PAST INTERNAL CLASSIFICATIONS OF CYPRINODONTIFORM FISHES

Cyprinodontiform fishes, as a whole or in part, have been the subject of various revisionary studies, many of which have included a formal reclassification. Together, these works may be characterized as studies in recognition of diversity, rather than in elucidation of interrelationships. From Garman's (1895) summary of all members to Sethi's (1960) discussion of primarily the oviparous cyprinodontids, reclassifications have focused on the description of differences, rather than of the derived similarities, among groups of cyprinodontiforms. The major classifications are summarized in table 3.

Garman attempted a synopsis of cyprinodontiforms; however, he had included the characin *Neolebias* and the cyprinoid *Fundulichthys* in the group. As a result, his diagnosis was general enough to apply to almost any group of soft-rayed fishes with a single dorsal fin. Aside from these shortcomings, however, Garman's summary of cyprinodontiform subgroups has remained little changed in subsequent reclassifications.

Garman divided the Cyprinodontes Gill (1865) (=Cyprinodontoidea of Rosen, 1964) into eight subfamilies. The known genera of goodeid fishes were included in the subfamily Cyprinodontinae, along with *Neolebias*. The poeciliid fishes were the sole constituents of the subfamilies Poeciliinae and Belonesocinae. *Jenynsia* and *Anableps* were each placed in their own subfamilies, Jenynsiinae and Anablepinae, respectively.

Cyprinodontids were divided among the Cyprinodontinae and the remaining three subfamilies. The monotypic Orestiasinae contained the genus *Orestias*; the known cyprinodontines constituted the remainder of the Cyprinodontinae.

Garman's Nothobranchiinae consisted of two African genera, *Haplochilichthys* and the aplocheiloid *Nothobranchius*. The remainder of the cyprinodontids, including the fundulines and South American aplocheiloids and *Fundulichthys*, together formed the subfamily Haplochilinae. The name of the type genus, *Haplochilus*, was a corrected spelling of *Aplocheilus* McClelland. This spelling change was not valid under the International Code of Zoological Nomenclature and was not used in subsequent revisions. However, the names *Haplochilus* and *Haplochilichthys* persist as identifications in

TABLE 3

**Major Classifications of Cyprinodontiform Fishes**

| Garman (1895) | Regan (1911) | Jordan (1923) | Hubbs (1924) | Myers (1931) | Myers (1955) | Sethi (1960) |
|---|---|---|---|---|---|---|
| Cyprinodontinae | Characodontinae | Characodontidae | Goodeidae | Goodeidae | | |
| | | Goodeidae | | | | |
| | Cyprinodontinae | Cyprinodontidae | Cyprinodontidae | Cyprinodontidae | Cyprinodontidae | Cyprinodontidae |
| | | | | Cyprinodontinae | Cyprinodontinae | Aphaniidae |
| Haplochilinae | Fundulinae | Cyprinodontidae | Fundulinae | Fundulinae | | |
| Nothobranchiinae | Fundulinae | | | Fundulini | Fundulinae | Fundulidae |
| | | | | Rivulini | Rivulinae | Aplocheilidae |
| | | | | Aplocheilini | Oryziatinae | Oryziatidae |
| | | | | Aplocheilichthyini | Procatopodinae | Aplocheilichthyidae |
| | | | | | Pantanodontinae | omitted |
| | | | | Lamprichthyinae | omitted | Aplocheilichthyidae |
| Orestiasinae | Orestiinae | Orestiidae | Orestiinae | Orestiatinae | Orestiatinae | Orestiatidae |
| Poeciliinae | Poeciliinae | Poeciliidae | Poeciliidae | Poeciliidae | | |
| Belonesocinae | Poeciliinae | | | | | |
| | | | Anablepidae | | | |
| Jenynsiinae | Jenynsiinae | Fitzroyidae | Jenynsiinae | Jenynsiidae | | |
| Anablepinae | Anablepinae | Anablepidae | Anablepinae | Anablepidae | | |

many collections. The name *Haplochilus* has been used to refer to fishes in such genera as *Epiplatys, Pachypanchax, Fundulus, Aphyosemion,* and *Oxyzygonectes* as well as *Aplocheilus*. Similarly, *Haplochilichthys* has been used to reference fishes in any of the procatopine genera, not solely *Aplocheilichthys*.

In Regan's (1911) reclassification of the order Microcyprini, the two subfamilies of poeciliids were united into the subfamily Poeciliinae. He separated the goodeids from the cyprinodontines and placed them in their own subfamily, the Characodontinae. Thus, with Regan's work, the four viviparous families were separated from the oviparous cyprinodontids. The precedent for treating oviparous and viviparous cyprinodontiforms separately in systematic revisions was established, and has remained virtually unchallenged until the present study.

The only concrete statements regarding the interrelationships of the five currently recognized families were made by Hubbs (1924) and Regan (1929), and these were in direct opposition. Hubbs grouped Jordan's Fitzroyidae (which he corrected to Jenynsiidae) and Anablepidae together into the family Anablepidae, and Jordan's Characodontidae and Goodeidae into the family Goodeidae. His action concerning the Goodeidae has remained unchallenged. However, the grouping together of *Anableps* and *Jenynsia* was rejected by Regan (1929) who placed *Anableps* in the Poeciliidae. Myers (1931) effectively avoided the problem by reverting to the placement of the two genera in monotypic families. Most recently, Miller (1979) has criticized the inferred relationship of the two, and considered *Anableps* to be more closely related to the Poeciliidae than to any other group of cyprinodontiforms.

Since Hubbs's work, reclassification of cyprinodontiforms has focused on the division of the Cyprinodontidae (encompassing the Cyprinodontinae and Fundulinae) into a variety of subgroups which have undergone elevations or reductions in rank.

Myers (1931) treated the oviparous cyprinodontids and *Oryzias*. His definition of the family consisted of the following characters: occipital condyles present on both basioccipitals and exoccipitals, no modifications of the anal fin into an intromittent organ, oviparous, premaxillaries distinct from maxillaries and protractile or not, and never more than 65 scales in a lateral series.

The definition, however, is not consistent with the distribution of characters among all cyprinodontids. More importantly, all the characteristics are primitive, and are found generally among teleost fishes. Thus, Myers (1931) effectively described the fishes of the family Cyprinodontidae as cyprinodontiforms that lack the prominent specializations of the viviparous groups. That is, no derived [unique] characters of the family were given to unambiguously define it as a monophyletic group.

Myers (1931) divided the family into four subfamilies, and further divided the largest, the Fundulinae, into four tribes.

The tribe Fundulini was restricted to the North American fundulines and their presumed relatives. The tribe Rivulini is coextensive with the aplocheiloids as discussed throughout the present paper.

Together, the tribe Aplocheilichthyini and subfamily Lamprichthyinae are coextensive with the procatopines. Similarly, the subfamily Orestiatinae consisted solely of the genus *Orestias*.

Eigenmann (1920) suggested that the North American *Empetrichthys* was the closest relative of *Orestias* based on the fact that both lack pelvic fins and fin supports, and have fleshy bases of the dorsal and anal fins. As a result, the two genera constituted the membership of the Orestiidae and Orestiinae of Jordan (1923) and Hubbs (1924), respectively. Myers (1931), however, supported the idea that *Empetrichthys* was more closely related to *Fundulus*, and placed it in his tribe Fundulini where it has remained until this study.

The final tribe, Aplocheilini Bleeker, consisted of a single genus, the ricefish *Oryzias* which Myers and contemporaries referred to as *Aplocheilus*. Fishes now commonly referred to the genus *Aplocheilus* were referred to as members of the genus *Panchax,* in the Rivulini. The confusion over the available names for these genera, all of the Indo-Malaysian region, was eliminated by Smith (1938) who demonstrated that *Panchax* was an objective synonym of *Aplocheilus,* and that *Oryzias* was the proper name for the ricefish. However, there was enough time for the name *Panchax* to become established as a common name for most of the aplocheiloid fishes, and it is still casually employed.

Earlier, Myers (1924c) pointed out that *Fundulichthys* Bleeker, a name applied to a specimen known only from an illustration, referred to a cyprinoid.

Berg (1940) substituted the name Cyprinodontiformes for the Microcyprini. He divided the order into two superfamilies, an oviparous Cyprinodontoidea including the families Cyprinodontidae and Adrianichthyidae, and a viviparous Poeciloidea, including the Goodeidae, Poeciliidae, Jenynsiidae, and Anablepidae. The adrianichthyid fishes, comprising the genera *Adrianichthys* and *Xenopoecilus,* were associated with the Cyprinodontiformes since their transfer from the Beloniformes (=Exocoetoidei) by Weber and de Beaufort (1922). However, because of its poor representation in collections (the monotypic *Adrianichthys* known only until recently from the single holotype), the family has gone virtually ignored in revisions. Rosen (1964) placed it along with *Oryzias,* which he elevated to family rank, and the Horaichthyidae, in the superfamily Adrianichthyoidea.

Myers (1955), again treating the oviparous killifishes and *Oryzias,* elevated each of his tribes of 1931 to subfamily rank. He acknowledged the correction of the use of the name *Aplocheilus* for *Oryzias* by elevating the rank of the tribe Aplocheilini to the subfamily Oryziatinae. A new subfamily Pantanodontinae appeared to include the single genus and species *Pantanodon podoxys* described in Myers (1955) by name only. An eighth subfamily, the Lamprichthyinae, was omitted from the list presumably inadvertently.

The oviparous killifishes were treated again by Sethi (1960) who elevated the ranks of these groups yet again. The oviparous cyprinodontids were classified in six families. *Oryzias,* included in the study, was also placed in its own family. The procatopines and *Lamprichthys* were grouped together in the family Aplocheilichthyidae.

*Aphanius* and its allies were removed from the subfamily Cyprinodontinae of Myers and placed in their own family, the Aphaniidae. Thus the Cyprinodontidae of Sethi consisted solely of *Cyprinodon* and its New World relatives.

The Pantanodontinae was inexplicably omitted from Sethi's study, as were other unique cyprinodontid genera such as *Oxyzygonectes, Chriopeoides, Cubanichthys,* and *Rivulichthys.* Also in 1970, Roberts created yet another subfamily, the Fluviphylacinae, to include a single genus and species, *Fluviphylax pygmaeus* (Myers and Carvalho). This genus was also disregarded by Sethi. Therefore, the most comprehensive and also most widely accepted classification of oviparous killifishes is that listed in table 2. The eight subfamilies are grouped together in a single family, the Cyprinodontidae.

The relationship of the subfamilies to each other and to the families of viviparous killifishes has never been formally treated before this study. In fact, Sethi's grouping of the Lamprichthyinae and procatopines represented the only alignment of subgroups of cyprinodontids since Garman (1895). Revisions of the viviparous killifishes have focused on the interrelationships of included genera or species, but have presented no more than informal remarks about the relationship of the considered family to another viviparous family or to the cyprinodontids.

Hubbs and Turner (1939), in a revision of the Goodeidae, emphasized the structural differences between the family and other cyprinodontiforms. More recently, Miller and Fitzsimons (1971) proposed several defining characters of the family (some of which are found among the oviparous cyprinodonts), and synonymies of several genera, yet made no statement as to the relationship of the goodeids to other cyprinodontiforms.

Rosen and Bailey (1963) provided a comprehensive discussion of the relationships of the family Poeciliidae to other cyprinodontiforms, yet came to no firm conclusions. They suggested that the closest relative of the poeciliids is perhaps another viviparous killifish; however, they stressed the fact that modifications for viviparity among the four families were not alike, except for the similar gonopodial structure of *Jenynsia* and *Anableps,* the intrafollicular development of poeciliids and *Anableps,* and the presence of trophic processes in goodeids and *Jenynsia.* In addition, Rosen and Bailey maintained that poeciliids were more like some oviparous than viviparous cyprinodontiforms in general body form and osteology; however, they did not suggest a group of cyprinodontids which could possibly be a close relative of the poeciliids.

Rosen and Bailey classified the Poeciliidae in three subfamilies: the Tomeurinae Eigenmann, containing just one genus and species, *Tomeurus gracilis*; the Xenodexiinae Hubbs, also containing just one genus and species, *Xenodexia ctenolepis*; and, the Poeciliinae, containing all other members of the family.

Structurally, *Tomeurus* is much like other poeciliids; however, it diverges strongly in the elaborate modifications of the gonopodium, and also in that it is the only oviparous poeciliid. (Internal fertilization results in the laying of a fertilized egg.) These differences, and also the remarkable similarity of the form of the gonopodium to that of the oviparous *Horaichthys,* an adrianichthyoid, led Nikol'skii (1954) to propose that the two genera, each classified in its own family, be united into one superfamily, the Tomeuroidea. Kulkarni (1948) however, suggested that on the basis of overall osteological similarity, *Horaichthys* was closer to *Oryzias* than *Tomeurus.* This conclusion has been supported by all recent workers on both poeciliids and adrianichthyoids (e.g., Rosen, 1964, 1973a; Rosen and Parenti, MS). The alignment of *Tomeurus* with the poeciliids is also supported by the present study.

Miller (1979), in discussing the relationships of *Anableps dowi,* supported the alignment of *Anableps* with the poeciliids, citing as evidence of close relationship the retention of the embryos in modified ovarian follicles during the entire developmental period, and the fact that the first three anal rays are unbranched in both. However, he made no formal reclassification and maintained that *Anableps* was so distinct that it should remain in its own family.

Alignments of one subfamily of cyprinodontids to another have been suggested by a number of workers (e.g., Ahl, 1924, 1928; Hoedeman and Bronner, 1951; Miller, 1955a; Uyeno and Miller, 1962).

Ahl (1924, 1928) considered solely the African cyprinodontid genera of the Rivulinae and Procatopodinae, which he believed formed a natural group.

Hoedeman and Bronner (1951, p. 1) made recommendations for the alteration of cyprinodontiform classification. They constructed the tribe Profundulidi to include the Old World genera *Kosswigichthys* and *Valencia,* and the North and Central American fundulines *Profundulus* and *Adinia.* The tribe was regarded as unnatural by Miller (1955a) who suggested that the Fundulinae and Cyprinodontinae be merged. Each of these four genera is regarded as a member of a different subgroup in the phylogenetic analysis of the present study.

Miller (1956), in describing *Cualac,* a new genus of cyprinodontids, stated that it was intermediate between the Fundulinae and North American Cyprinodontinae. He reiterated his previous suggestion that the two groups together comprise the subfamily Cyprinodontinae, claiming that they were probably artificially separated on the basis of dental morphology.

Later, however, Uyeno and Miller (1962) supported Sethi's conclusion that the two groups remain separated in a classification. They listed a series of characters from Sethi (1960) by which the fundulines could be distinguished from the cyprinodontines: the presence of parietals; neural arches of the first vertebra not fused to skull, and therefore, taking no part in the articulation of the vertebral column to the skull; the presence of occipital condyles; and, the lack of a gap between the first and second vertebrae. These characters are, however, as Myers's defining characters of the Cyprinodontidae, primitive for atherinomorph fishes. Thus, it is not just the superfamily and families which are poorly defined, but the subfamilies as well that lack precise definitions and, therefore, need to be supported or refuted as monophyletic groups of genera.

Foster (1967) presented a summary of his conclusions regarding atherinomorph phylogeny in a branching diagram. The Pantanodontinae was removed from the cyprinodontiforms and placed as a close relative of the adrianichthyoids. Within the cyprinodontids, he recognized six subfamilies (the Fluviphylacinae Roberts obviously omitted), concluding that the Rivulinae and Orestiatinae were sister groups primitive to other cyprinodontiforms, excluding *Pantanodon*.

The Procatopodinae and Lamprichthyinae were similarly depicted as sister groups primitive to the four viviparous families and the Fundulinae and Cyprinodontinae. Foster considered the fundulines to be most closely related to the Anablepidae (presumably including *Jenynsia*) which together formed the sister group of the poeciliids. This subgroup, in turn, was assessed as being most closely related to the Cyprinodontinae and Goodeidae, represented as sister groups.

This analysis was based on an assessment largely of overall similarity for a group of 16 or more characters, including those of the osteology, behavior and development.

Foster presented no formal reclassification of the atherinomorph fishes. He therefore retained the subfamily rank for *Pantanodon* even though he considered it to be more closely related to the adrianichthyoids. However, in spite of such inconsistencies related to the level at which he was approaching the problem, this work represented for the first time a precise although informal statement about the interrelationships of the four viviparous families and their relationship to the subfamilies of the Cyprinodontidae was presented. It is noteworthy also for including the implicit statement of the nonmonophyletic nature of the family Cyprinodontidae.

However, Foster's treatment, like the others, grouped the families and subfamilies mainly on overall similarity without regard to the primitive or derived nature of characters. The family Cyprinodontidae and also the cyprinodontiform fishes as a whole, as indicated by Foster's removal of *Pantanodon*, are left to be formally defined as monophyletic groups or to have their monophyly refuted. Similarly, the viviparous families remain to be unambiguously defined on the basis of derived characters unique to them and not found in other cyprinodontiforms.

Thus, to accomplish the stated objectives of this study, the four viviparous families are treated as four more genera of cyprinodontiform fishes, the monophyly of each being supported or rejected. Furthermore, the reclassification of cyprinodontiforms presented in this study is based on an attempt to define the major groups of genera and represent their hierarchical relationship, rather than to obscure such relationship by basing the rank of a taxon on subjective criteria of uniqueness.

## DERIVED CHARACTERS OF CYPRINODONTIFORMS

The Cyprinodontoidea has been recognized since the definition of the family Cyprinodontidae by Gill (1865). However, the failure by him and subsequent workers to define the Cyprinodontidae rigorously has resulted in the uncritical inclusion with them of the ricefish genus *Oryzias* until Rosen (1964) placed it in its own family and suggested its close relationship to the adrianichthyoid fishes. Inadequate definition of the Cyprinodontidae also is responsible for the unsupported placement of *Pantanodon* with adrianichthyoids by Foster (1967).

Previous workers attempting to define the superfamily (e.g., Regan, 1911; Hubbs, 1924) have included characters either primitive for atherinomorph fishes or shared by a number of its subgroups. As a result, the superfamily has never been unambiguously defined as a monophyletic group (in the sense of Hennig, 1966).

The current study has revealed that all fishes of the superfamily Cyprinodontoidea may be distinguished from all other teleost fishes by the following derived features.

CAUDAL FIN: A series of derived characters within the caudal fin is found relatively unmodified in all cyprinodontiforms. Externally, the fin is rounded or truncate, although in males of several aplocheiloid genera, procatopines, and the South American *Orestias*, there are often extensions of the dorsal and ventral caudal rays. In no case are there incipient lobes; although, Miller (1979) reports that in males of *Anableps microlepis*, lower caudal rays are often grouped together forming a lobelike structure. Branched caudal rays typically number eight or more.

Internally, the supports of the caudal fin are symmetrical (fig. 2E). There are two hypural plates, one above and one below corresponding to fused hypurals 3, 4, and 5 and 1 and 2, respectively. In some species of *Epiplatys* and *Aplocheilus*, the upper hypural plate is divided in two, apparently representing the unfused hypurals 4 and 5 (fig. 2D).

Within the cyprinodontiforms, fusion of the hypural plates into a so-called hypural fan (following the terminology of Rosen, 1964) occurs within several monophyletic groups of genera (e.g., fig. 2F).

There is just one epural which mirrors in shape and position the autogenous parhypural. There are no separate ural centra. The hypochordal musculature is also absent (Rosen, 1964).

This formation of a symmetrical caudal fin in unique among teleost fishes. The esocoid *Umbra limi* has a caudal fin which is externally unlobed and rounded. Yet, an examination of the internal structure reveals that the external symmetry is effected by a complex of two epurals, one uroneural, five unfused hypurals, and two separate ural centra, the second of which is dorsally offset to the first (fig. 2A). In addition, there are fewer than eight branched caudal rays.

Among other groups of atherinomorphs, there are lobate caudal fins exclusively. The atherinoid *Menidia beryllina* (fig. 2B) has a caudal skeleton which is asymmetrical in having two epurals which are relatively smaller than the opposing parhypural. The divided hypural plate has a larger dorsal segment. *Oryzias* (fig. 2C) has an asymmetrical caudal fin support in which two small epurals oppose the single, large parhypural. The hypural plate is divided into subequal dorsal and ventral segments.

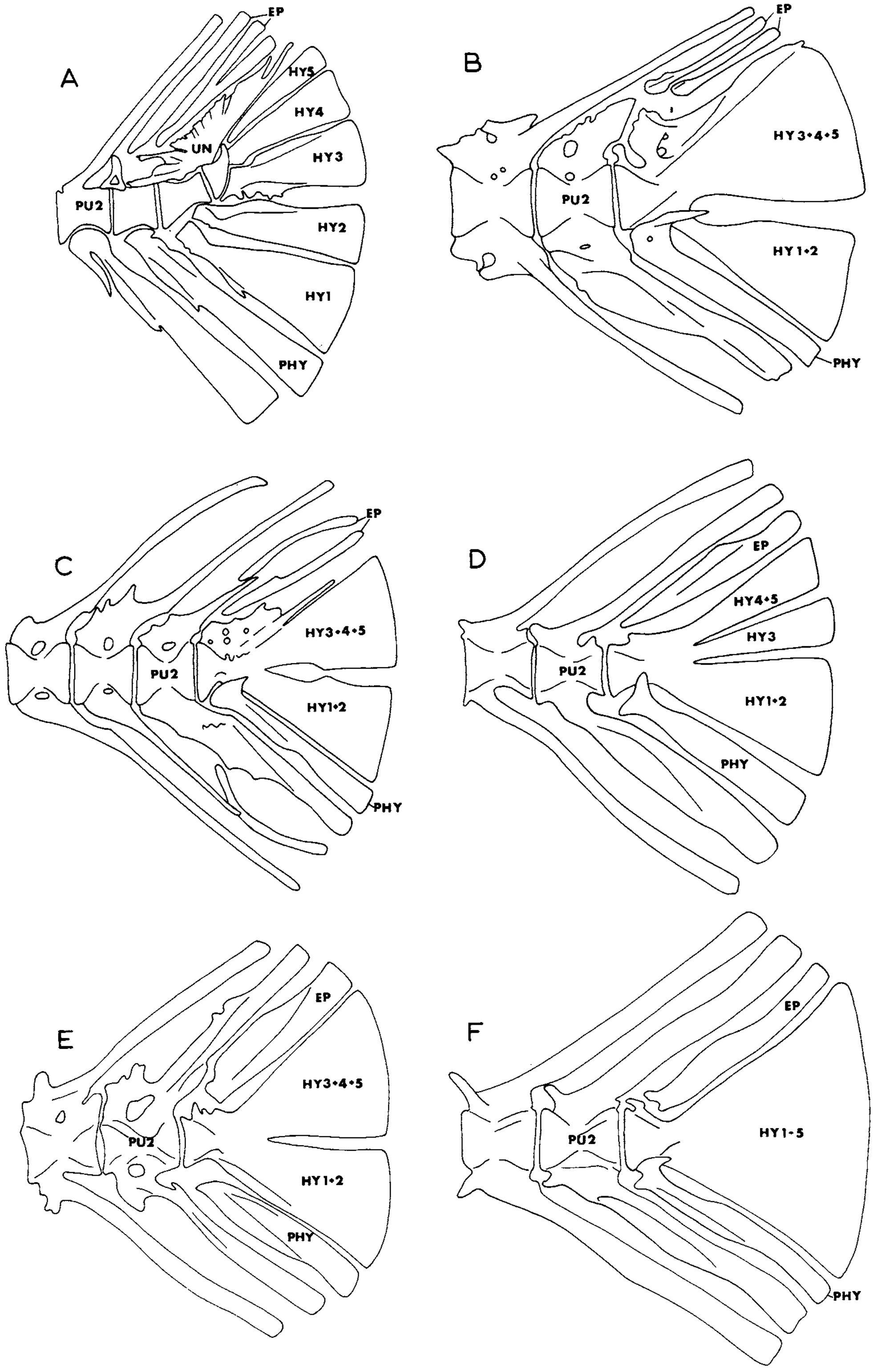
FIRST PLEURAL RIB: Typically among the atherinomorph fishes, the first pleural rib arises on the parapophysis of the third vertebra. Occasionally the rib is borne on the parapophysis of the fourth vertebra in males of the genus *Ceratostethus*, and both males and females of the genus *Gulaphallus*, both phallostethoid fishes in the suborder Atherinoidei (Roberts, 1971).

Within the cyprinodontiforms, the first pleural rib is borne on the parapophysis of the second vertebra. In the funduline genus *Adinia* there is a pleural rib on the parapophysis of the first vertebra; this condition is considered to be apomorphic for the genus.

Rosen (1964) followed Myers (1928a) in stating that the first pleural rib of phallostethoids arose on the parapophysis of the second vertebra, and therefore suggested a close affinity between the phallostethoids and cyprinodontiforms. However, Roberts (1971) has shown this to be a misidentification of the state in phallostethoids. Examination of several genera of phallostethoid fishes as part of this and other studies has supported Roberts' contention. Therefore, the first rib arising on the parapophysis of the second vertebra is a characteristic unique to cyprinodontiforms.

JAW STRUCTURE: The protrusible upper jaw of the atherinomorph fishes differs from that of other acanthopterygians in the lack of a ball and socket joint between the autopalatine and the maxilla, and the absence of crossed rostral ligaments (Rosen, 1964).

The absence of a ball and socket joint prevents the premaxillaries from being locked in the protruded position by the autopala-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tines upon the opening of the mouth. However, the premaxillaries may still be held protracted by contraction of the superficial division of the adductor mandibulae (A1) (Alexander, 1967a, 1967b), which inserts on the middle of the distal arm of the maxilla.

Crossed rostral ligaments run from the left autopalatine and the right autopalatine to the heads of the right and left premaxillaries, respectively. These ligaments, along with a pair of ethmomaxillary ligaments, typify the mechanism of the protrusible upper jaw of acanthopterygians (Schaeffer and Rosen, 1961).

The atherinomorphs lack crossed rostral ligaments; thus, the forward movement of the premaxillaries is limited by contact with the maxilla. Among the atherinomorphs, Alexander (1967b) reports the presence of an ethmomaxillary ligament in the atherinoids *Atherina* and *Melanotaenia*, and the aplocheiloid *Aplocheilus*. He notes its absence in *Fundulus* and the poeciliid *Xiphophorus*.

The mechanism of protrusion of the upper jaw of cyprinodontiforms has been described in detail by Rosen (1964) and Alexander (1967a, 1967b). It is characterized by a two-part alveolar process of the premaxillaries. A distal part of the process is joined to an offset proximal part of the process, thus creating a wide bow, as illustrated in the aplocheiloid *Austrofundulus* (fig. 3A). In all cyprinodontoids, the process is primitively S-shaped (fig. 3B) as a result of the distal part of the process being strongly indented posteriorly.

At the posterior tip of the ascending processes of the premaxillaries is a large, free rostral cartilage. Among acanthopterygians, the rostral cartilage is typically firmly attached to the ventral surface of the tips of the ascending processes by connective tissue fibers, and, in addition, is sometimes wrapped around the tips of the processes. The median process of the maxillary head is bound by connective tissue fibers to the anterior end of the rostral cartilage.

The presumed function of the rostral cartilage is to prevent the independent movement of the premaxillaries, and also to prevent their rolling off the cranium when the mouth is opened (Alexander, 1967a, 1967b). However, since the maxilla functions as a brace during the forward movement of the premaxillaries in atherinomorphs, and the rostral cartilage is not present in all cyprinodontiforms, it appears that the rostral cartilage serves mainly as a restrainer of the independent movement of the premaxillaries.

Primitively, within most acanthopterygians and most atherinomorphs, in addition to being bound to the ascending processes of the premaxillaries, the rostral cartilage is attached to the median processes of the maxillary heads by connective tissue fibers. Alexander (1967b) reports that in atherinoids there is also often an attachment of the cartilage to the vomer and to the ethmoid cartilage.

Among cyprinodontiforms, variability in the states of degree of attachment of the rostral cartilage, size of the cartilage, its presence or absence, length of the ascending processes of the premaxillaries and presence or absence of the ethmomaxillary ligaments allows for the description of transition series of these characters and the delimitation of at least three distinct mouth forms within the group. (Sethi, 1960, referred to both the rostral cartilage and the mesethmoid as the mesethmoid; therefore, his descriptions of states of the mesethmoid are unreliable since they refer to either one or the other.)

The aplocheiloids share some similar upper jaw characteristics with the atherinoids. These are the presence of an ethmomaxillary ligament, the presence of a ligament from the internal hooks of the maxillaries to the rostral cartilage, and the presence of a meniscus between the premaxilla and maxilla. These

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FIG. 2. Diagrammatic representation of the caudal skeleton of A. *Umbra limi* (after Rosen, 1974); B. *Menidia beryllina*; C. *Oryzias latipes* (after Rosen, 1964); D. *Aplocheilus panchax*; E. *Aphyosemion gardneri*; F. *Fundulus heteroclitus*.

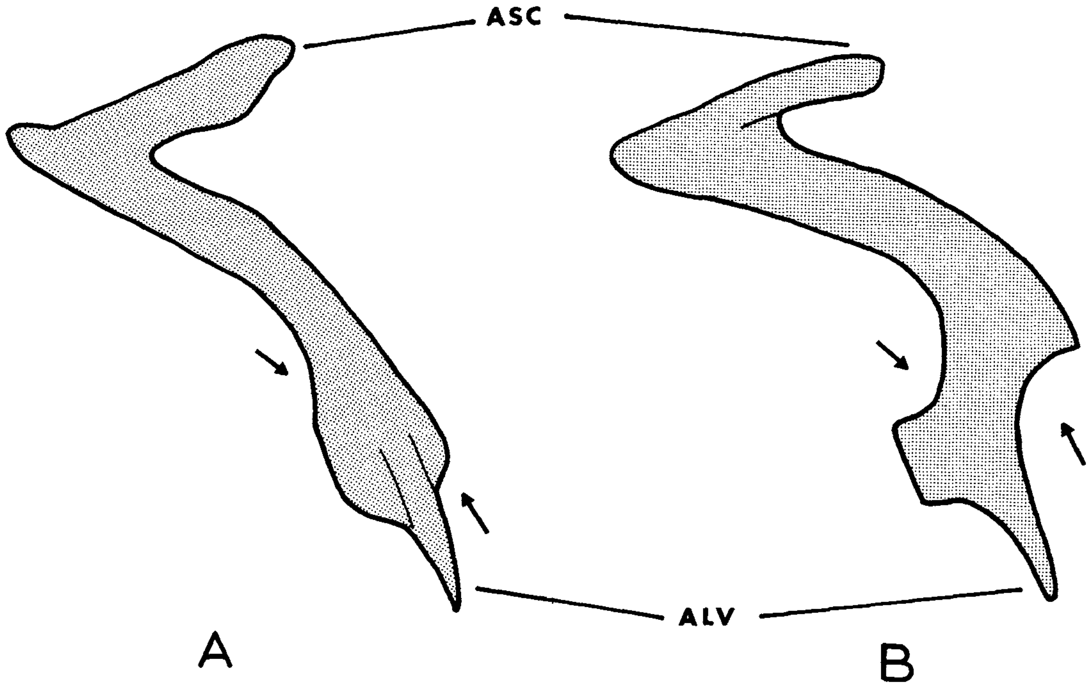

FIG. 3. Diagrammatic representation of premaxillary alveolar arm, lateral view, of A. *Austrofundulus transilis*; B. *Profundulus punctatus*. Arrows point to areas indented in cyprinodontoids to form S-shaped arm.

ligaments and the meniscus are absent in all cyprinodontoids.

The rostral cartilage in cyprinodontiforms, as stated, is free and not wrapped around the ascending processes of the premaxillaries as it is in most acanthopterygians. This permits the movement of the rostral cartilage relative to, rather than with, the ascending processes. In all aplocheiloids, the rostral cartilage is a large, disc-shaped element lying beneath the flat and broad ascending processes (fig. 4). In one cyprinodontoid genus, *Profundulus* (fig. 5B), the ascending processes are broad and the cartilage large, yet somewhat reduced relative to the aplocheiloid condition. It is further reduced in the fundulines (fig. 5C), and *Valencia* (fig. 5D).

Among remaining cyprinodontiforms (figs. 35, 39), the cartilage is present as a minute disc, or absent, whereas the ascending processes are shortened, or nearly absent as in *Anableps*, and held together by connective tissue fibers.

Thus, within the cyprinodontiforms there are three basic forms of the upper jaw and jaw suspension. The first, and apparently most primitive, is that of the aplocheiloids. The rostral cartilage is large and firmly attached to the broad premaxillary ascending processes. There are ligamentous attachments of the head of the maxilla to the rostral cartilage and of the maxilla to the ethmoid. The large size of the rostral cartilage and the presence of ligaments are assessed as primitive by comparison with an outgroup, the atherinoids, and to the percomorph fishes, in which these states are present.

There are three distinct states of the premaxillary ascending processes in cyprinodontiforms: flat and broad in aplocheiloids and *Profundulus*, long and narrow in *Fundulus* and related genera, and short and

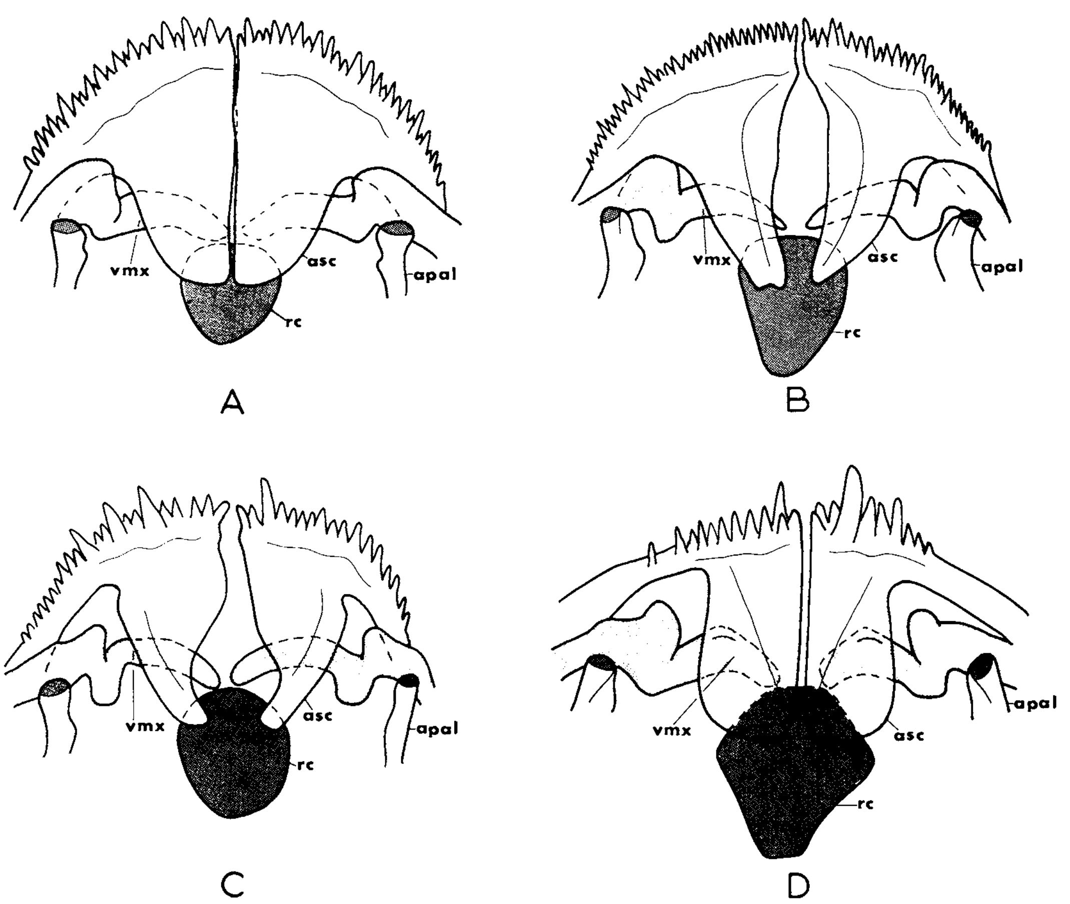

FIG. 4. Diagrammatic representation of the upper jaw in A. *Aplocheilus panchax*; B. *Pachypanchax playfairi*; C. *Aphyosemion petersi*; D. *Cynolebias whitei.*

pointed or triangular in all remaining cyprinodontiforms. Exceptions occur in *Anableps,* as mentioned, and in *Oxyzygonectes* in which the processes are enlarged. These exceptions are discussed in the phylogenetic analyses and generic diagnoses.

The size of the ascending processes in other atherinomorphs and acanthopterygians is variable; however, the general or most common state is for the processes to be long and narrow. This would suggest that the transition series for ascending processes is from a primitive state of long and narrow to flat and broad in one lineage, and to short and narrow in another. However, information from other systems clearly indicates that *Profundulus* is more closely related to cyprinodontoids than to aplocheiloids. Therefore, the flat and broad ascending processes are most parsimoniously assessed as the primitive state within the cyprinodontiforms. The short and pointed or triangular processes coupled with an extremely reduced, or in some cases absent, rostral cartilage, are defining characters of a large group of cyprinodontiforms encompassing the poeciliids, goodeids, *Jenynsia, Anableps, Oxyzygonectes,* the cyprinodontines, *Orestias, Cubanichthys, Chriopeoides,* and the procatopines.

In addition, in this group as well as in the

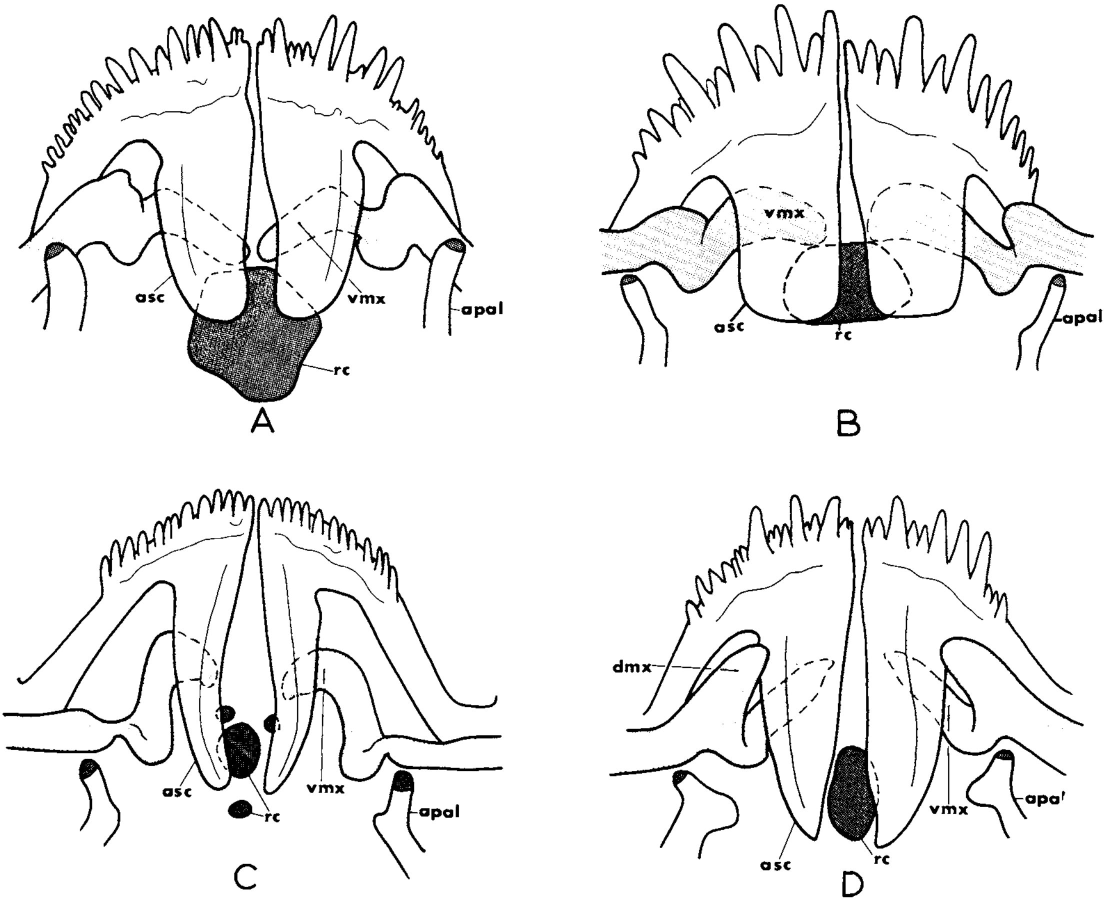

FIG. 5. Diagrammatic representation of the upper jaw in A. *Rivulus harti*; B. *Profundulus punctatus*; C. *Fundulus diaphanus*; D. *Valencia hispanica*.

Mediterranean *Valencia*, there is a dorsal extension of the maxilla over the ascending processes, which forms a cuplike process with the ventral extension. The short ascending premaxillary processes slide in and out of this maxillary cup. In primitive cyprinodontiforms the twisted maxilla extends ventrally under the premaxilla but not dorsally.

GILL ARCHES: Interarcual cartilages are found among the percomorph fishes (Rosen and Greenwood, 1976). The general condition is that found in the atherinoid genus *Melanotaenia*. A rod of cartilage extends between an uncinate process of the first epibranchial and the second pharyngobranchial. In contrast, the uncinate process is lacking in all cyprinodontiforms. The cartilage is subequal to the epibranchials in aplocheiloids, and extends between the posterior base of the first epibranchial and the second pharyngobranchial (fig. 6A). In cyprinodontoids, the cartilage and the first epibranchial are both present in the same position; yet, they are reduced to approximately half their length relative to the size of these elements in the aplocheiloids (fig. 6B).

The interarcual cartilage is present in all cyprinodontiforms except groups of procatopine and of aplocheiloid genera in which

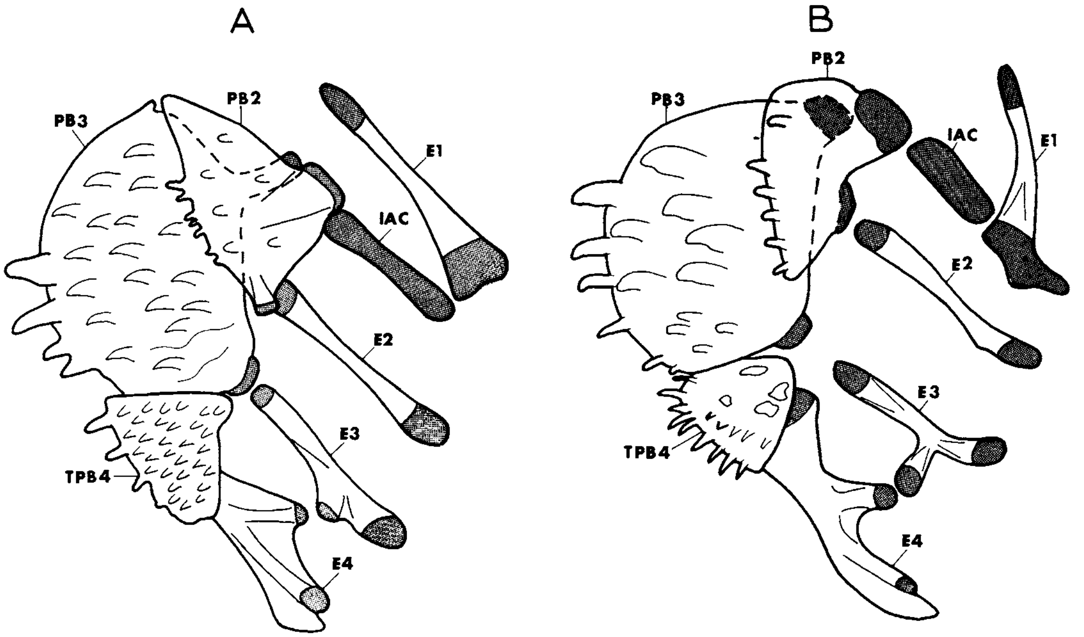

FIG. 6. Diagrammatic representation of dorsal gill arches, ventral view, A. *Austrofundulus transilis*; B. *Profundulus punctatus*.

other elements of the dorsal gill arches are present in a typical arrangement, and the interarcual cartilage is assumed to have been lost.

PECTORAL GIRDLE: The cyprinodontiform shoulder girdle typically has a first postcleithrum which is large and scale-shaped (figs. 7C, 8A, B). This is in contrast to the condition in atherinoids and exocoetoids in which the first postcleithrum is typically a slender bone (figs. 7A, B). Among cyprinodontiforms the first postcleithrum is absent, and therefore presumed lost, in poeciliids, most procatopines, *Leptolucania, Orestias, Rivulus* and its South American relatives and one species of *Anableps, A. dowi.*

There is another postcleithrum situated medial to the scapula and radials, and extending ventrally beyond the coracoid. This long, slender element is present in cyprinodontiforms. Rosen and Bailey (1963) interpreted this as a "secondary postcleithrum" in the poeciliids without discussing its homology to the second postcleithrum of lower teleosts. Roberts (1970) referred to it as the "first rib?" in his description of the osteology of the South American *Fluviphylax pygmaeus.* Sethi (1960) refers to the element only in an illustration in which it is labeled "PCL [Postcleithrum] 2."

Weitzman (1962) illustrated the shoulder girdle of the characin *Brycon meeki* which has three postcleithral elements. The third postcleithrum is comparable in shape and position to the so-called secondary postcleithrum of cyprinodontiforms. Therefore, I interpret these structures as homologues and conclude that the general condition for a cyprinodontiform is to have a large first postcleithrum, and a narrow third postcleithrum, with the second postcleithrum always lacking.

Also, the lowset pectoral fin, effected by a ventral position of the radials (e.g., fig. 7A, D), primitively distinguishes the cyprinodontiforms from all other atherinomorphs which have highset pectoral fins and more dorsally situated radials (fig. 7A, B).

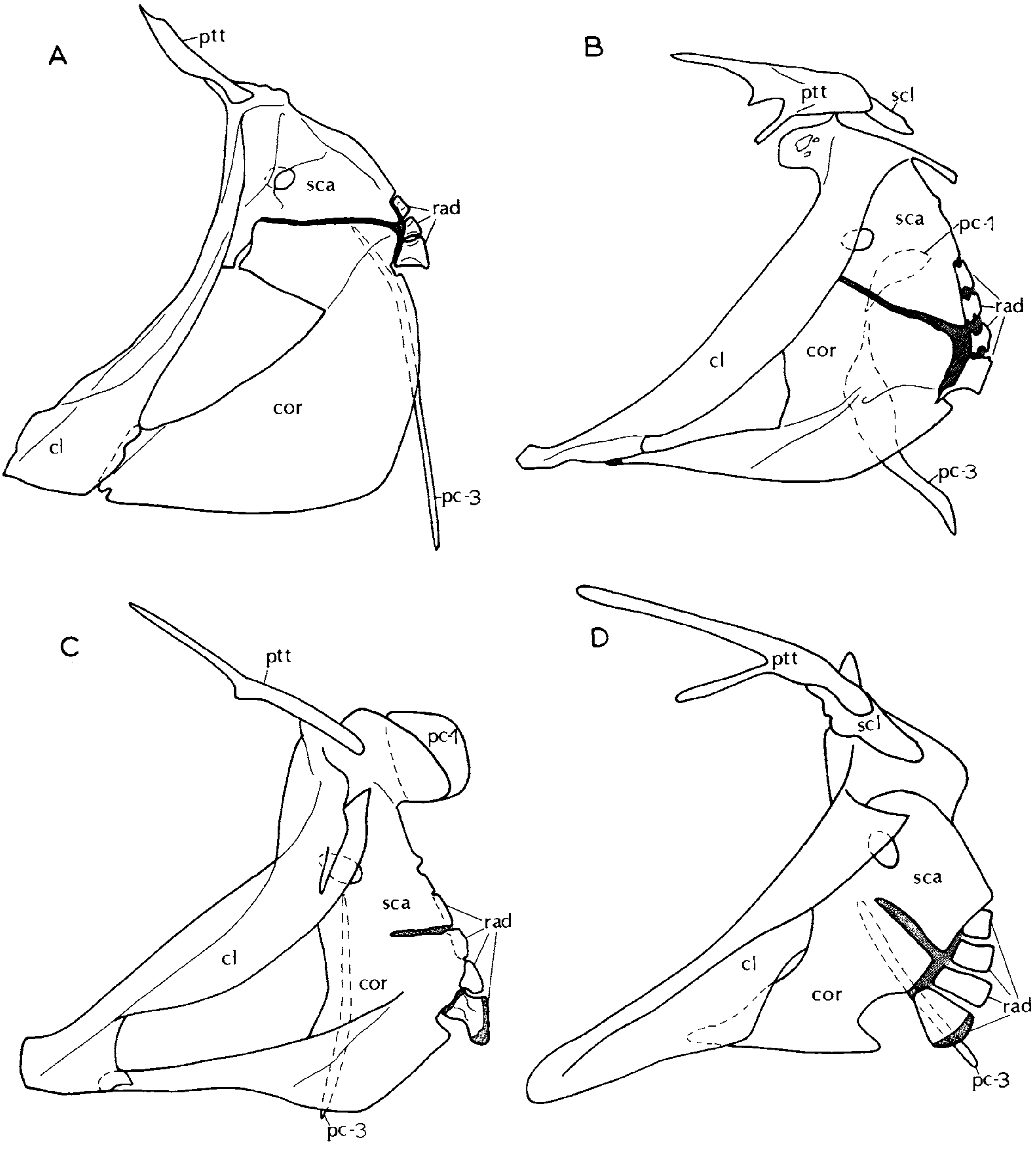

FIG. 7. Diagrammatic representation of left shoulder girdle of A. *Oryzias javanicus*; B. *Menidia menidia*; C. *Aplocheilus panchax*; D. *Rivulus harti*. Cartilage is stippled.

Highset pectoral fins within cyprinodontiforms occur in the poeciliids and procatopines (fig. 8C, D), and are interpreted as being secondarily derived. This is the most parsimonious interpretation of the condition of the shoulder girdle based on (1) a series of uniquely derived characters that indicate a close relationship between the poeciliids and procatopines, and (2) a series of derived characters that indicate that these two are

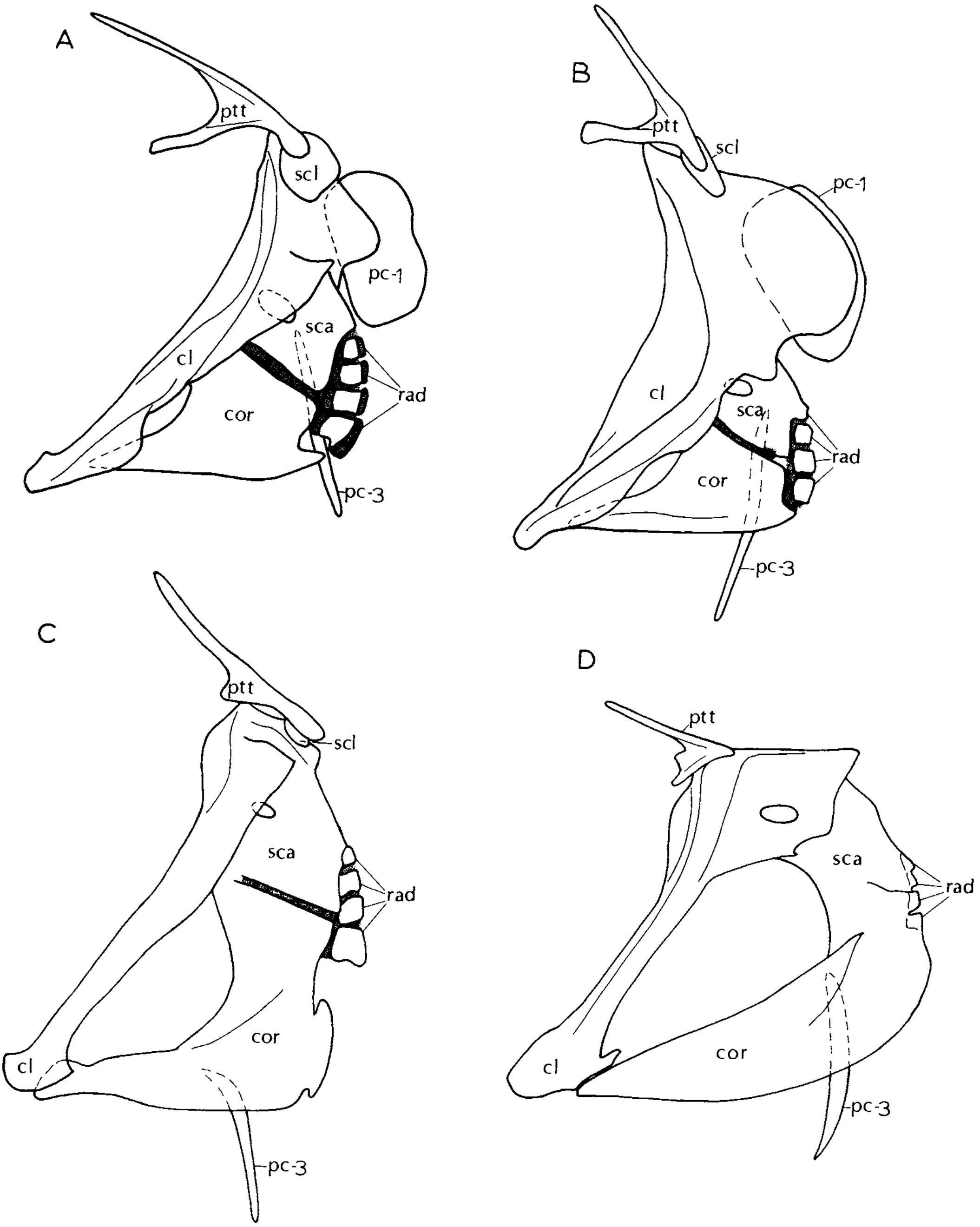

FIG. 8. Diagrammatic representation of left shoulder girdle of A. *Profundulus punctatus*; B. *Cyprinodon variegatus*; C. *Procatopus gracilis*; D. *Tomeurus gracilis*. Cartilage is stippled.

together more closely related to one group of cyprinodontiforms with lowset pectorals than to another, which also possesses lowset pectorals.

BREEDING AND DEVELOPMENT: Eggs of the oviparous atherinomorph fishes are distinguished by having long, chorionic filaments by which they attach to the spawning substrate, and conspicuous oil droplets (inferred to be secondarily lost in the suborder Exocoetoidei) (Foster, 1967). Cyprinodontoid eggs, in turn, are distinguished by their relatively longer development time and thickened chorion, the outermost egg membrane.

Thus, the egg of a typical oviparous cyprinodontiform may be characterized as large (some over 2.0 mm in diameter), containing several oil droplets and surrounded by a thick, filamentous chorion. A typical nonannual cyprinodont egg has a development time of 12 days or longer. Eggs of the atherinoid *Bedotia geayi* were observed in the laboratory to have a development time of about nine days. Development time is up to six months for eggs of fishes in true annual genera such as the South American *Cynolebias* and the African *Nothobranchius*. The thick chorion permits survival under conditions of desiccation during an extended development period, such as those typical of *Fundulus*.

The annual habit (first reported by Myers, 1942; then described in detail by Peters, 1965, and Wourms, 1963, 1964, 1967, 1972a, 1972b, and 1972c) is exhibited by a minority of the aplocheiloid species of tropical South America and Africa. Adults live for no more than one rainy season during which time they spawn. The eggs enter diapause and survive the dry period buried in the substrate. The fertilized eggs normally hatch at the onset of the subsequent rainy season; however, they have been known to survive dry periods of several years.

Foster (1967) reports that in the atherinoid *Melanotaenia* and in *Oryzias* spawning normally takes place without direct contact with a substrate. In addition, a large number of eggs are extruded at once. In contrast, all killifishes, with a few possible exceptions, spawn in contact with a substrate, and eggs are extruded one at a time. Spawning in a typical annual occurs daily from the onset of sexual maturity, which occurs as early as four to six weeks, until death.

Annual fish eggs enter three diapause stages prior to hatching (Wourms, 1972a). The first, termed Diapause I, occurs during the pre-embryonic stage. The cells of the blastodisc separate and disperse around the surface of the yolk sphere. Arrest lasts until the cells reaggregate to form the embryonic shield when the anterior-posterior axis of the embryo is established for the first time.

Diapause II occurs during the mid-somite stage about the time of formation of the heart tube. Diapause III occurs just prior to hatching. The embryo is fully formed and capable of hatching, yet does not. The embryo remains quiescent; its heart beat slows down and the characteristic turning of the embryo and associated beating of the pectoral fins within the chorion are slowed or cease. The duration of each of the diapause stages is controlled either by genetic or environmental factors, or an interplay of the two. Embryos in stage III have remained quiescent for more than six months (Wourms, 1964).

Previous workers have considered the annual habit to be uniquely derived within the annual killifish genera therefore suggesting that these fishes form a monophyletic group. The present study disagrees with this conclusion for two reasons: (1) On the basis of anatomical characters, certain true annuals are assessed as being more closely related to nonannuals than they are to other true annuals. (2) All cyprinodontiforms have a prolonged development time, and within genera that are not closely related to the aplocheiloids, survival of eggs through periods of desiccation has been demonstrated.

The first of these reasons is discussed fully in the phylogenetic analysis of cyprinodontiform genera. The second is given in support of the contention that the annual habit is no more than an exaggeration, due to extreme environmental fluctuations, of a capability of all cyprinodontiforms to survive stress that involves desiccation.

Foster (1967, p. 538) summarized the habitats of killifishes as: "If any generalization could be made about the ecology of killifishes, it is that they exploit niches mostly in ephemeral waters, places which are temporarily submerged by tides, floods from heavy rains, or similar causes."

The ability of nonannual killifish embryos to survive desiccation has been reported for a number of species within the North American genera *Fundulus* and *Cyprinodon.*

Harrington (1959) reported that populations of *Fundulus confluentus* in Florida have survived hatching delays of up to three months. Areas of the salt marsh habitat of this killifish are exposed to the air during the months of October through December. Also, Taylor, DiMichele and Leach (1977) observed that another estuarine *Fundulus, F. heteroclitus,* often spawns during the high night tide. Eggs are thus stranded in the substrate up to a week after expected hatching time; hatching is delayed until reimmersion occurs.

In an effort to test the generality of the ability of cyprinodont eggs to survive desiccation, F. Douglas Martin (personal commun.) exposed eggs of *Cyprinodon* to the air and found that they can survive through hatching; although, on the average, they are less successful at hatching than *Fundulus* species. This may indicate that the ability to survive periods of desiccation is primitive for cyprinodontiforms and is lost in the more advanced genera such as *Cyprinodon.*

The first two diapause stages have not been demonstrated in nonannuals; however, the ability to survive pre-hatching desiccation in the nonannuals appears to be comparable to Diapause III.

Turner (1966) reports that a collection of *Pantanodon podoxys* has been made in Africa from stagnant pools. The common cyprinodontiforms in the vicinity were two species of the annual *Nothobranchius* which were present in similar pools. No permanent body of fresh water was found that could be inferred to have originally formed the pools. Such circumstances suggest that *Pantanodon* may be an annual, and therefore that annualism among cyprinodontiforms is not restricted to the aplocheiloids, but is perhaps a general characteristic of those cyprinodontiforms which inhabit ephemeral waters.

The use of a potential annual lifestyle as a defining character of the cyprinodontiforms is confounded by the fact that the atherinoid *Leuresthes tenuis* spawns in conjunction with the tidal water level fluctuations so that the eggs are incubated while exposed to the air (Clark, 1925). This suggests that the ability to survive desiccation is a derived character for the atherinomorph or some larger group of fishes. However, the generality of this condition and its concordant developmental alterations for other groups of fishes awaits further description. Therefore, the early and regular breeding habit and long developmental period, coupled with the ability to survive desiccation, is considered to describe a unique developmental pattern of cyprinodontiform fishes.

## PHYLOGENETIC ANALYSIS

The monophyly of each of the five families of cyprinodontiform fishes has been tested. A preliminary examination revealed that each of the four viviparous families is monophyletic and can be unambiguously defined, although not with all of the characters previously used to define them.

The Cyprinodontidae, however, as currently constituted, cannot be defined as a monophyletic group. The alternative hypothesis is that some oviparous cyprinodontiforms are more closely related to the viviparous cyprinodontiforms than they are to other oviparous forms.

Therefore, the genera of cyprinodontid fishes are used as a basis for a cladogram of all cyprinodontiforms. The poeciliids, goodeids, *Jenynsia,* and *Anableps* are treated as additional genera incorporated into the overall scheme.

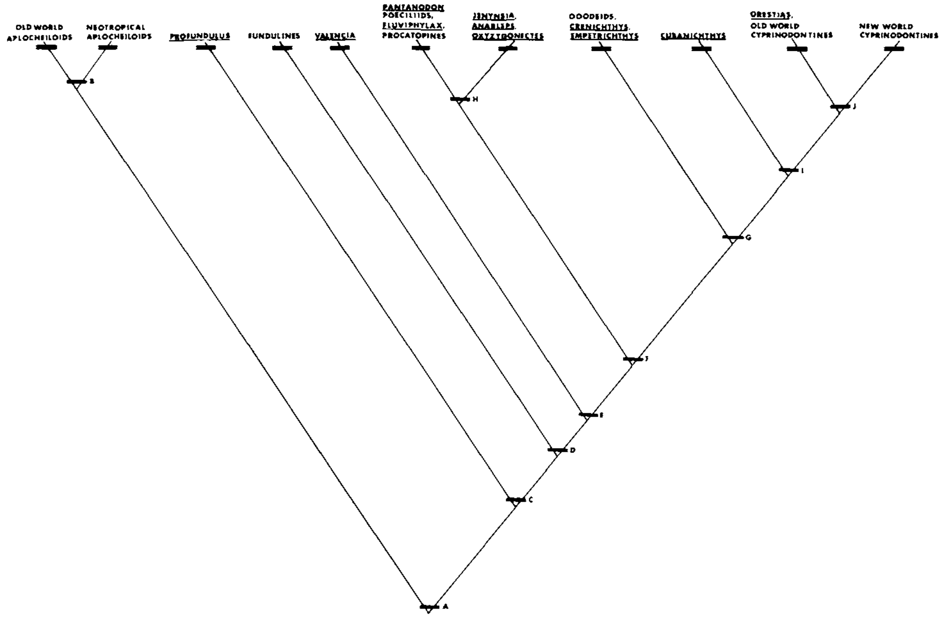

FIG. 9. Cladogram of major groups of cyprinodontiforms. Derived characters: Node A: symmetrical caudal fin, externally rounded or truncate, internally with one epural opposing a similarly shaped parhypural, hypural plates symmetrical; alveolar arm of premaxilla; interarcual cartilage from base of first epibranchial to second pharyngobranchial; first pleural rib on parapophysis of second vertebra; lowset pectoral girdle with scale-shaped first postcleithrum; early breeding habit and long developmental period; Node B: attached orbital rim; cartilaginous mesethmoid; close-set pelvic fin supports; narrow and twisted lacrimal; broad anterior end of basihyal; tubular anterior naris; reduced cephalic sensory pore pattern; pigmentation pattern (see text); Node C: two ossified basibranchials; loss of the dorsal hypohyal; reduced interarcual cartilage; head of autopalatine offset to main axis and with posterior flange; anterior ventral extension of the autopalatine; loss of the metapterygoid; premaxilla with a posterior indentation of the alveolar arm; dentary expanded medially; loss of the first dorsal fin ray; loss of an ethmomaxillary ligament; loss of a ligament from the maxillaries to the rostral cartilage; loss of a meniscus from between the premaxilla and maxilla; Node D: premaxillary ascending processes narrow or greatly reduced in adults; rostral cartilage reduced or absent; inner arms of maxillaries not abutting the rostral cartilage; lateral ethmoid with reduced facet for articulation of autopalatine; Node E: maxilla with straight proximal arm; large dorsal process of the maxilla directed over the premaxillary ascending process; Node F: ascending processes of the premaxillaries short and narrow; dorsal processes of maxillaries rounded or reduced; nasal expanded medially (or secondarily reduced); Node G: lateral ethmoid expanded medially and lying perpendicular to the frontal; reduced autopterotic fossa; enlarged inclinators of the anal; Node H: maxilla with expanded distal arm (or secondarily reduced); parasphenoid with expanded anterior arm; dorsal process of maxilla with a distinct lateral indentation; elongate retroarticular; pouch created by scales surrounding urogenital opening of females. Node I: dorsal processes of the maxillaries expanded medially, nearly meeting in the midline and possessing a distinct groove; lateral arm of maxilla robust; toothplate of fourth pharyngobranchial reduced. Node J: uniserial outer teeth: second pharyngobranchial offset to third; parietal absent; Meckel's cartilage expanded posteriorly; transverse processes of vertebrae reduced and cup-shaped. For defining characters and relationships within terminal taxa, see text and figures 20, 25, 75, 81, 83, 87, and 89.

In this discussion of phylogenetic relationships, the vernacular names as summarized previously are used for suprageneric categories. At the conclusion of the phylogenetic analysis, a reclassification is presented. New group names in the classification are used in the systematic account and biogeographic analysis which follow.

The results of the phylogenetic analysis are best presented in a cladogram (fig. 9). Limits and definitions of the recognized genera are presented in this discussion and formally in the systematic accounts.

The cladogram is a hierarchic representation of the relationships among genera and suprageneric categories which are being proposed. The representation is of the most parsimonious distribution of derived characters and character states. Hypothesized convergences are discussed along with the proposed derived characters.

The characters for the most inclusive node are the derived characters of the cyprinodontiforms (Group A of fig. 9) discussed in the previous section. These are the unique formation of a symmetrical caudal fin; the first pleural rib arising on the parapophysis of the second vertebra, rather than on that of the third; a derived type of protrusible jaw; a unique form and position of the interarcual cartilage; the lowset pectoral fins with a large, scale-shaped first postcleithrum; and a unique pattern of breeding and development.

The cyprinodontiforms are readily divided into two subgroups, the currently recognized cyprinodontid subfamily Rivulinae (the aplocheiloids), and all other cyprinodontiforms, termed the cyprinodontoids. Since these groups are both large and quite distinct, their interrelationships are discussed separately.

## APLOCHEILOIDS (GROUP B)

The aplocheiloid killifishes comprise over 500 species in 44 nominal genera and subgenera. Within the aplocheiloids, there are two groups of genera, the Old World aplocheiloids comprising *Epiplatys, Aplocheilus, Pachypanchax, Nothobranchius, Aphyosemion* and their included subgenera; and, the New World or Neotropical aplocheiloids comprising the genera *Rivulus, Trigonectes, Rivulichthys, Rachovia, Pterolebias, Simpsonichthys, Campellolebias, Cynolebias, Austrofundulus, Cynopoecilus, Terranotus* and their included subgenera.

CHARACTER ANALYSIS: Orbital rim: The orbital rim is attached to some degree in all aplocheiloids. In all the Neotropical aplocheiloids and in the African genera *Aphyosemion, Fundulosoma, Nothobranchius* and *Epiplatys,* the covering of the eye is continuous with that of the head along the perimeter of the orbit. In the remaining aplocheiloids, those species of the genera *Aplocheilus* and *Pachypanchax,* the rim is attached on the lower half of the orbit, and is apparently folded under the expansion of the orbit dorsally. In the cyprinodontoids, and other atherinomorph fishes, the orbital rim is free all along its perimeter.

The partially attached rim of *Aplocheilus* and *Pachypanchax* initially appears to be an intermediate state between the completely free rim and the fully attached rim. However, because of its apparent folding under the frontals, and also because the Old World aplocheiloids are assessed as a monophyletic group on the basis of a series of other characters, the partially attached rim is most parsimoniously assessed as secondarily derived in *Aplocheilus* and *Pachypanchax.*

Mesethmoid: The atherinomorph fishes exhibit a derived condition of the ethmoid region as described by Rosen (1964). The mesethmoid is typically represented by two ossified discs which are angled toward each other at their anterior limit to create a wedge.

In all aplocheiloids examined, the mesethmoid is totally cartilaginous, except for the presence of some small ossification centers in several larger specimens of *Cynolebias.*

The mesethmoid is generally a large ossified structure in most other cyprinodontiforms; however, it is cartilaginous in the procatopines, and in the cyprinodontines of the Anatolian region (e.g., in *Aphanius* and *Kosswigichthys*). Because the last two groups are members of the well defined, monophyletic cyprinodontoids, the cartilaginous mesethmoid is hypothesized to be independently

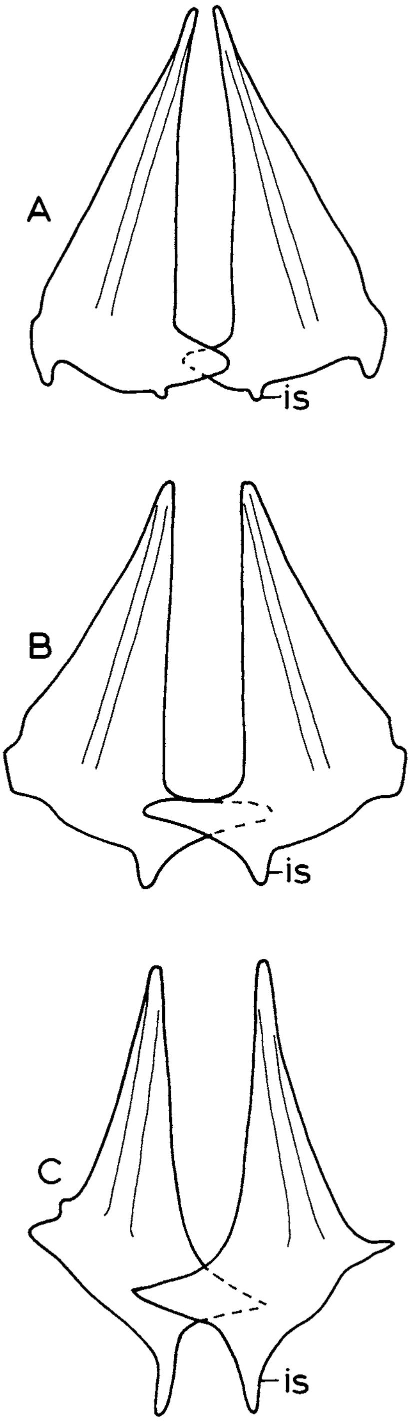

FIG. 10. Diagrammatic representation of pelvic girdles of A. *Aplocheilus panchax;* B. *Jenynsia lineata;* C. *Aphanius fasciatus.*

derived several times within the evolution of cyprinodontiform fishes.

Pelvic Girdle: The pelvic girdles of atherinomorphs are found united, as in *Menidia* and other atherinoids, or widely separated, as in *Oryzias*. When united, the pelvic bones are joined medially by overlapping processes. In cyprinodontiforms, they are so united. In the cyprinodontoids, as well as in *Menidia,* the anterior part of the girdle is perpendicular to the medial overlapping processes (fig. 10B, C). In contrast, the aplocheiloids (fig. 10A) have pelvic bones which are set close together as a result of the medial processes being reduced.

Gill Arches: Aplocheiloids generally exhibit the primitive state of the gill arch characters for cyprinodontiform fishes. That is, there is a large interarcual cartilage running from the base of the first epibranchial to the side of the second pharyngobranchial, to which it attaches by a ligament. There are also rosette-shaped gill rakers which have been described by Myers (1927) as being unique to the aplocheiloids. This type of gill raker, however, is found in *Menidia* and other atherinoids, as well as many cyprinodontoids. Therefore, it is hypothesized to be a primitive character of a group larger than the cyprinodontiforms and is not a defining character of the aplocheiloids.

One characteristic of the gill arches unique to the aplocheiloids is the broad anterior end of the basihyal (fig. 11A). This is typically a slender bone with a cartilaginous cap which is only slightly flared in cyprinodontoids (fig. 11B) and other atherinomorphs. In aplocheiloids, however, the bone and its associated cartilage approach the shape of an equilateral triangle, especially in the Old World aplocheiloids which have just a small ossified basihyal and large cartilaginous segment (fig. 11A). In the Neotropical aplocheiloids, the ossified segment is much larger. The large cartilaginous anterior end of the basihyal gives the aplocheiloids their characteristic large "tongue" which is readily visible upon opening the mouth.

Lacrimal: Another derived character that defines the aplocheiloids as a monophyletic group is the shape of the lacrimal. In all aplocheiloids, the lacrimal is a narrow and

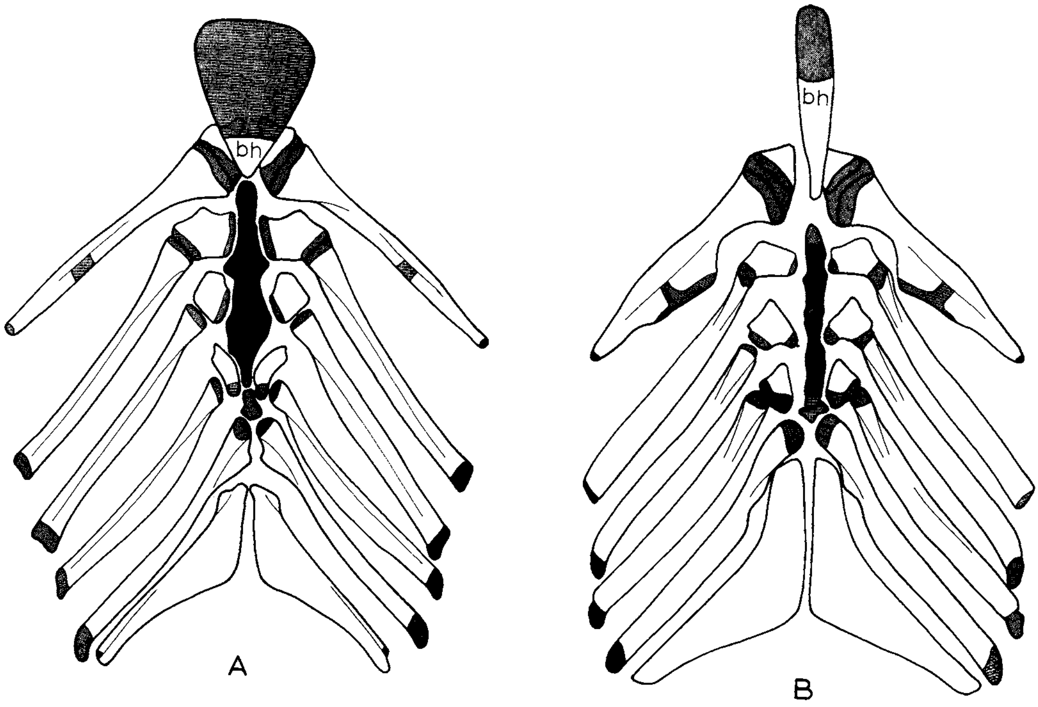

FIG. 11. Diagrammatic representation of ventral gill arches of A. *Nothobranchius melanospilus;* B. *Cubanichthys cubensis.* Cartilage is stippled.

twisted bone which often carries a distinct sensory canal (fig. 12A). This is in contrast to the wide and flat lacrimal typically found in the atherinomorph fishes. In *Menidia* (fig. 12B) the lacrimal is flattened and expanded ventrally. In *Poecilia* (fig. 12C) the lacrimal is also flat and wide. The lacrimal is reduced among the cyprinodontoids in the genus *Pantanodon*; however, the preorbital distance is wide compared to that of the aplocheiloids, and the narrow lacrimal of *Pantanodon* is considered secondarily derived. Among the aplocheiloids, the canal of the lacrimal is apparently reduced along with the sensory canals of other dermal bones in the Neotropical aplocheiloids, as discussed below.

Anterior Naris: In all atherinomorph fishes minus the exocoetoids, the anterior and posterior naris are represented by two separate openings. The anterior naris is typically a small opening just posterior to the fold of skin surrounding the maxilla, whereas the posterior naris is typically a small slit just anterior and dorsal to the orbit. The anterior naris of all aplocheiloids is surrounded by a distinct tube of skin which projects anteriorly over the upper jaw (fig. 13). A distinct tubular naris is found among the cyprinodontoids in *Cubanichthys* and *Anableps,* and is considered to be independently derived in the aplocheiloids and in each of these advanced genera. In all other cyprinodontiforms, the anterior naris never has such a fleshy extension.

Cephalic Sensory Pores and Squamation: Gosline (1949) surveyed sensory pore patterns in the cyprinodontiforms as a whole with an emphasis on the goodeids and *Fundulus.* Hoedeman (1958, 1974) in his surveys of head-scale patterns among cyprinodontiforms was responsible for bringing attention to this associated character. Rosen and Mendelsohn (1960) surveyed the sensory pore as well as head-scale patterns among the poeciliids. It has been observed that both sensory pore and head-scale patterns are correlated. That is, their separate analyses

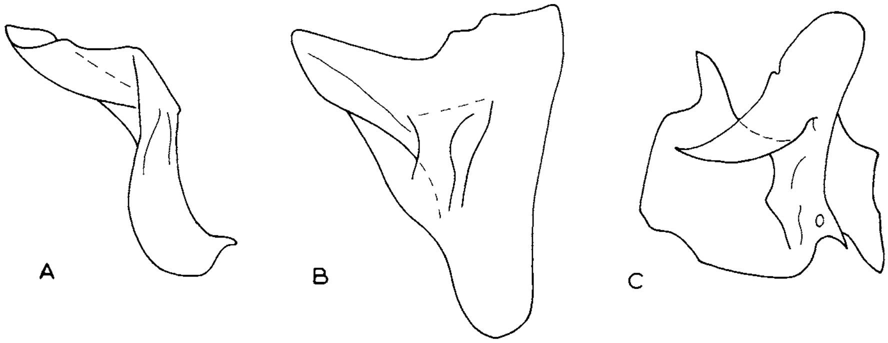

FIG. 12. Diagrammatic representation of left lacrimal of A. *Rivulus harti*; B. *Menidia menidia*; C. *Poecilia vivipara*. Anterior is to the left.

could introduce redundancy into this study. Therefore, the two systems are discussed together.

There is much taxic variability as well as ontogenetic variation within these systems. The cephalic sensory system starts out in ontogeny as a series of open grooves over which skin grows leaving the grooves open to the surface only by a series of pores. Gosline also noted for three species of *Fundulus* that neuromasts of the juvenile pattern are covered over as the individual grows and replaced by a covered canal with pores.

Hoedeman (1958) referred to replacement of two scales by one larger scale as a fusion; however, Roberts (1970) suggested instead that it was the formation of fewer scale precursors that resulted in such changes. Without developmental studies on comparative scale formation, this difference seems moot; however, such replacements will not be referred to as fusions because this implies a process for which there is no evidence.

As a consequence of variability within these systems, it is only the most general characteristics which may be incorporated into a higher level phylogenetic analysis. Also, because of the ontogenetic changes, it is usually the maximum development of pores and scales that is reported as the general state for a species or genus. The generalized sensory pore and squamation pattern for cyprinodontiforms is as in the cyprinodontoid, *Jenynsia lineata* (fig. 14A, B, C). There are seven preopercular pores, three lacrimal pores, four mandibular pores, and seven supraorbital pores. This pattern is judged to be the primitive pattern for cyprinodontid fishes based on personal observation, and data from Gosline (1949) and Wiley (personal commun.). The numbering system for the pores follows Gosline.

Departures from the general pattern (fig. 14) occur both with respect to the continuity of canals between pores, and therefore, the number of pores, and the number and position of scales.

Among the aplocheiloids, the sensory pores of the head are reduced to a series of neuromasts, as in *Rivulus harti* (fig. 13C), a Neotropical aplocheiloid, and in *Epiplatys sexfasciatus* (fig. 13B), and Old World species. Among the cyprinodontoids, the sensory pores of the head are often reduced, but not replaced by neuromasts.

Sexual Dimorphism: All cyprinodontiforms show marked sexual dimorphism. Males typically are elaborately pigmented and frequently have elongated rays in the unpaired and the pelvic fins.

All cyprinodontiforms exhibit sexual dimorphism in size. In aplocheiloids, males are larger than females. In the cyprinodontoids, the reverse is true: females are larger than males. The exception in the cyprinodontoid killifishes occurs within the procatopines and *Pantanodon* and *Fluviphylax* in which the males are always larger than the females. Among the silversides, in genera such as *Bedotia, Melanotaenia, Gulaphallus* and

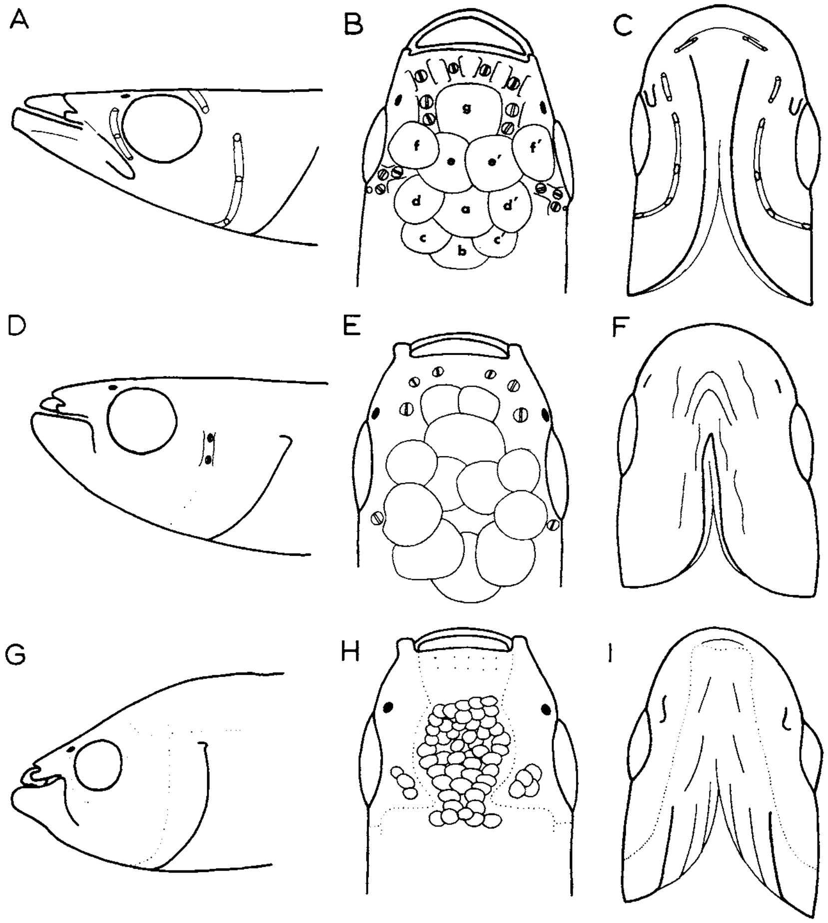

FIG. 13. Diagrammatic representation of cephalic sensory pores and squamation. *Epiplatys sexfasciatus*: A. lateral view of lacrimal and preopercular pores, B. dorsal view of neuromasts and squamation, C. ventral view of mandibular and preopercular pores; *Rivulus harti*: D. lateral view of reduced pore pattern, E. dorsal view of neuromast and squamation pattern (lettering of scales corresponds with b.), F. ventral view of covered branchiostegal region; *Cynolebias elongatus*: G. lateral view of minute neuromast pattern, H. dorsal view of neuromast pattern, I. ventral view of neuromast pattern and branchiostegal region.

others, the males are larger than the females. In at least one species related to *Menidia beryllina*, females are larger than males. In exocoetoids the males are also larger than females, or of approximately the same size. Thus, the most general condition among the atherinomorph fishes appears to be that males are larger than females. If so, the primitive state for the cyprinodontiforms is for males to be larger than females. In this case, the aplocheiloids retain the primitive condition and the small size of the males is a derived character of cyprinodontoids. The large male in procatopines is, therefore, a secondarily derived condition.

No general pattern of pigmentation has been discovered among aplocheiloids. Some pigmentation patterns do, however, occur in some of the more primitive genera of both the Old World and Neotropical groups, and these are assessed as derived for the aplocheiloid fishes. These include a caudal ocel-

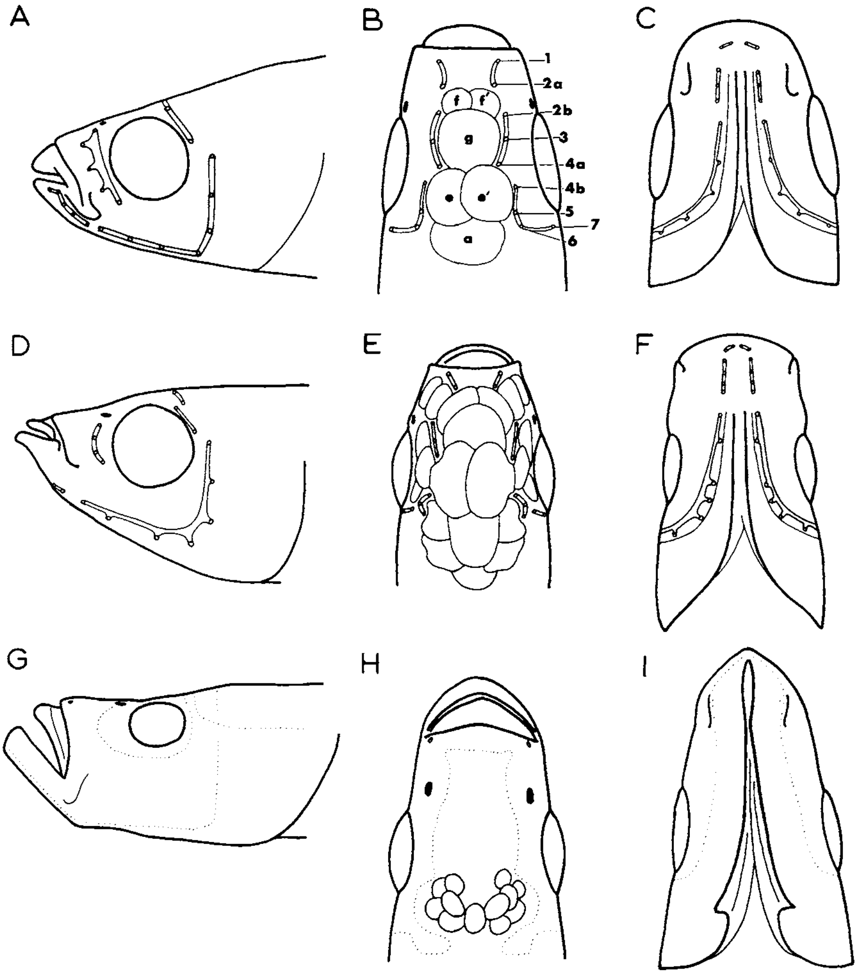

FIG. 14. Diagrammatic representation of cephalic sensory pores and squamation. *Jenynsia lineata*: A. lateral view of preopercular and lacrimal pores, B. dorsal view of supraorbital pores and squamation, C. ventral view of mandibular and preopercular pores; A generalized poeciliid (after Rosen and Mendelsohn, 1960): D. lateral view of preopercular and lacrimal pores, E. dorsal view of supraorbital pores and squamation pattern, F. ventral view of mandibular and preopercular pores; *Orestias cuvieri*: G. lateral view of minute neuromast pattern, H. dorsal view of minute neuromast pattern, I. ventral view of neuromast pattern and embedded urohyal.

lus in females; bars running across the ventral surface of the head, commonly called "throat bars"; and a band, normally of white or yellow, on the dorsal and ventral base of the caudal.

The caudal ocellus, or "*Rivulus* spot" has been used to diagnose fishes of the genus *Rivulus*. In females of all nominal species of the genus, there is a black blotch (fig. 54), or sometimes discrete spot (e.g., as in *R. marmoratus*) dorsally on the caudal fin base. Such an ocellus, however, is also found in some females of the genus *Aphyosemion*. Assuming that the spots are homologous, the character is a synapomorphy of the aplocheiloids, and no longer defines *Rivulus* as a monophyletic genus.

Throat bars are most prominent in species

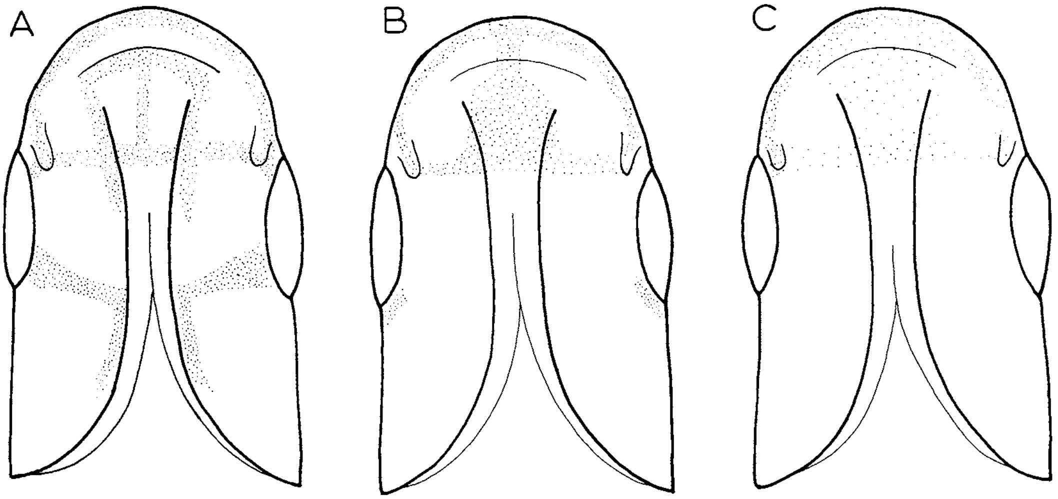

FIG. 15. Diagrammatic representation of ventral view of head to show throat bars in A. *Epiplatys dageti*, B. *Epiplatys chaperi*, C. *Aplocheilus panchax*.

of the genus *Epiplatys* (fig. 15A, B), although they are also a conspicuous component of the pigmentation patterns of species of *Aphyosemion* and *Aplocheilus* (fig. 15C), and to a lesser extent *Rivulus* and *Pachypanchax*. These are often found in conjunction with a line of pigment on the lower lip; however, this line of pigment is found among many cyprinodontoids, as well as in many aplocheiloids which do not possess conspicuous throat bars (e.g., in *Nothobranchius*).

A horizontal band of yellow or white, rarely blue, on the dorsal and ventral bases of the caudal fin is a distinctive component of the pigmentation patterns of the males of most species of *Rivulus, Aphyosemion, Fun-*

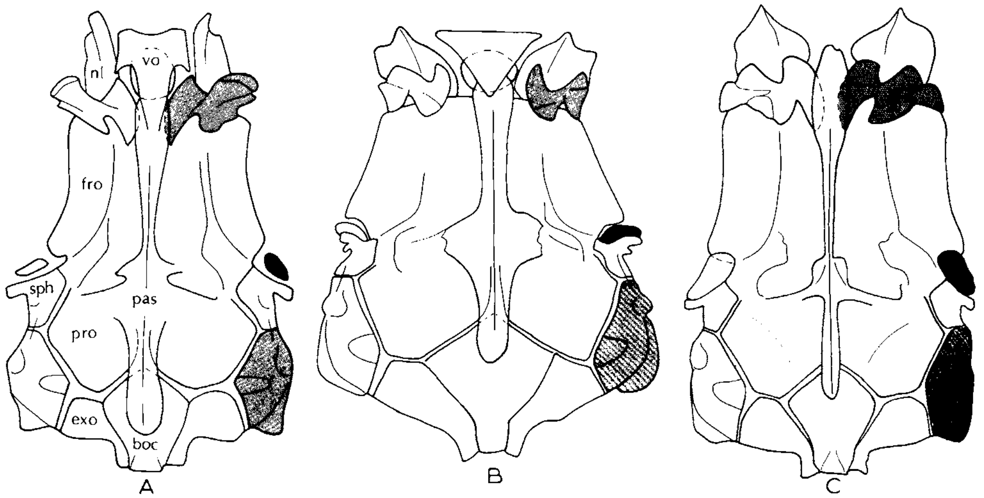

FIG. 16. Diagrammatic representation of a ventral view of skull in A. *Fundulus heteroclitus*, B. *Tomeurus gracilis*, C. *Aplocheilichthys johnstoni*. Lateral ethmoid is cross-hatched, dermosphenotic blackened, autopterotic stippled.

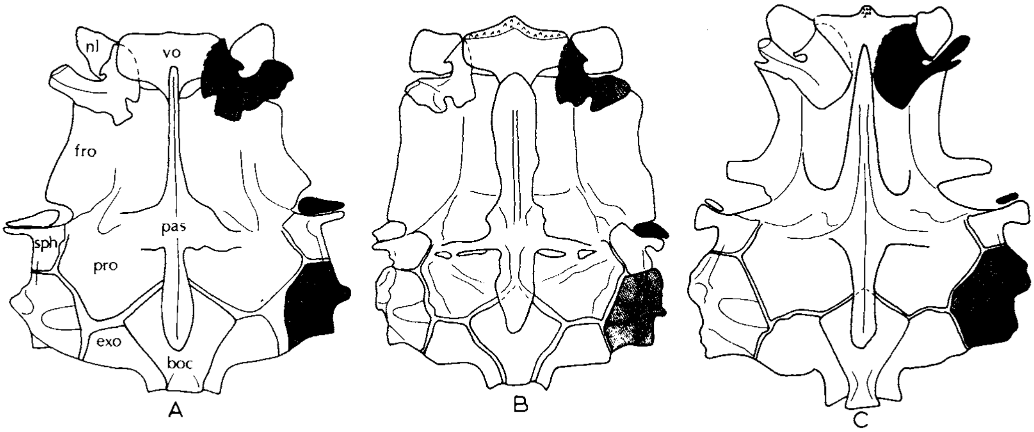

FIG. 17. Diagrammatic representation of a ventral view of skull in A. *Aphyosemion occidentale*, B. *Aplocheilus panchax*, C. *Rivulus harti*. Lateral ethmoid is cross-hatched, dermosphenotic blackened, autopterotic stippled.

*dulosoma*, and to a lesser extent in species of the genus *Epiplatys* (e.g., in *Epiplatys fasciolatus*). Such a band is found only on the ventral base of the caudal in species of the nominal genera *Rachovia* and *Neofundulus*. In at least two species of *Aphyosemion*, *A. celiae* and *cinnamomeum*, the light yellow bars extend along the posterior margin of the fin to form one continuous band (Radda, 1979).

The difficulty in determining the primitive or advanced state of these pigment patterns is analogous to determining whether sexual dimorphism involving large males or large females is primitive. The general color patterns just described are normally retained in preserved specimens since the majority involve dark pigments, rather than the unstable or water and alcohol soluble pigments of yellow, blue and red. In an analysis done at the level of the current study, intrageneric variation has not been the subject of concentrated study. However, elaborate color patterns of large males, distinguished by the derived characters listed here, distinguish aplocheiloids from all other cyprinodontiform fishes. Other types of elaborate male color patterns occur within the poeciliid fishes among cyprinodontoids. Elaborate male coloration does not occur in the hypothesized primitive poeciliid, *Tomeurus gracilis*, however.

Position of the Vomer: The posterior extension of the vomer typically lies ventral to the anterior arm of the parasphenoid in all cyprinodontoids (fig. 16), as well as other atherinomorphs. In contrast, the posterior extension of the vomer lies dorsal to the anterior arm of the parasphenoid in all aplocheiloids (fig. 17), a clearly derived condition.

## SUMMARY OF DERIVED CHARACTERS

1. Attached orbital rim.
2. Cartilaginous mesethmoid.
3. Close set pelvic girdles.
4. Broad anterior end of the basihyal.
5. Narrow and twisted lacrimal.
6. Tubular anterior naris.
7. Reduced cephalic sensory pores.
8. Males more elaborately pigmented than females.
9. Posterior extension of the vomer dorsal to the anterior arm of the parasphenoid.

## NEOTROPICAL APLOCHEILOIDS

The aplocheiloids are hypothesized to comprise two monophyletic groups of genera: one a solely Old World group, and the second Neotropical and north temperate. The latter range from southern Florida and the Bahamas, through Central America, and southward to Paraguay (fig. 18). They are currently classified in 13 nominal genera and subgenera: *Rivulus, Rachovia, Austrofundulus, Trigonectes, Rivulichthys, Pterolebias, Terranotus, Neofundulus, Leptolebias, Campellolebias, Cynopoecilus, Simpsonichthys,* and *Cynolebias,* five of which are monotypic.

In all revisions or discussions of all or part of the Neotropical aplocheiloids, they have been treated as a monophyletic group (e.g., Regan, 1912; Myers, 1927; Weitzman and Wourms, 1967; and Taphorn and Thomerson, 1978), although the group has never been formally defined. Regan (1912) listed the following characters to distinguish the three then known genera *Rivulus, Pterolebias,* and *Cynolebias,* and his newly named *Cynopoecilus* from other fishes then classified in the Fundulinae: snout short, margin of eyes not free, gill membranes separate, mouth wide and transverse with the premaxillaries protractile, lower jaw prominent and oblique, teeth subconical and arranged in bands, with one large outer row, pectorals placed low, and pelvics not far in advance of the anal.

The majority of these characters are either derived for the aplocheiloids as a group, or for all cyprinodontiforms. Others, such as "gill membranes separate" may refer to certain characters inferred in this study to be derived.

Myers (1927) in a revision of Neotropical aplocheiloids cited the attached orbital rim and rosette-shaped gill rakers as defining characters, characters which clearly define a larger group of fishes.

Weitzman and Wourms (1967) emphasized the ambiguity of the definitions of the genera of Neotropical aplocheiloids, and remarked on the states of certain characters, such as the close-set pelvic fins in all members, but did not compare these with other cyprinodontids in an effort to present defining characters of the group. Similarly, Taphorn and Thomerson (1978) who treated only those species of the genera *Rachovia* and *Austrofundulus,* describing *Terranotus* as new, concentrated on enumerating differences among nominal genera, rather than describing derived similarities in an effort to determine interrelationships of the genera.

The question still remains, therefore, if the Neotropical and Old World aplocheiloids form distinct monophyletic groups of genera, or whether some Neotropical genera are more closely related to some Old World genera than to other Neotropical genera. References to the overall similarity of the African *Nothobranchius* to the South American *Cynolebias* have been made continuously in the aquarium literature (e.g., Stoye, 1947; Scheel, 1968). Furthermore, and perhaps more importantly, the idea that annualism is a uniquely derived character (Wourms, 1972a) suggests that Neotropical annuals are more closely related to the Old World annuals than to the fishes of the predominantly nonannual genus *Rivulus.*

Taphorn and Thomerson (1978) stated they agreed with Weitzman and Wourms's (1967) conclusion that the Neotropical aplocheiloids such as *Austrofundulus* and *Rachovia* were derived from a *Rivulus*-like ancestor, but *Cynolebias* and *Terranotus* were not included in this endorsement of Weitzman and Wourms' position.

Thus, the definition of the Neotropical aplocheiloids as a distinct monophyletic group is a step toward our understanding of the evolution of the annual lifestyle, as well as toward a definition of the problems that remain in aplocheiloid systematics.

CHARACTER ANALYSIS: Shoulder Girdle: The shoulder girdle of Neotropical aplocheiloids is distinguished from that of other aplocheiloids by lacking the first postcleithrum (fig. 7D). Other cyprinodontiforms have a large, scale-shaped first postcleithrum, as in

FIG. 18. Distributional limits of Neotropical aplocheiloids.

*Aplocheilus* (fig. 7C). The first postcleithrum is present in all Old World aplocheiloids examined.

Cephalic Sensory Pores and Squamation: A series of derived characters related to the sensory canal system of the head, including squamation patterns, opercular and branchiostegal membranes, and development of dermal bones carrying sensory canals serve to define the Neotropical aplocheiloids as a monophyletic group. For example, the typical condition of the branchiostegal and opercular membranes in atherinomorph fishes is that exhibited by the Old World aplocheiloid *Epiplatys* (fig. 13C). Several branchiostegal rays are visible through a clear membrane which is separate from that overlying the opercular region. The preoperculum, which is not united by a membrane to the operculum ventrally, carries a distinct sensory canal which is open externally as a series of pores. There is a fold of skin covering the throat region between the dentary and the urohyal. The throat region, including the branchiostegal membranes, is generally not covered with scales. In contrast, the membranes covering the opercular region and the branchiostegal rays are totally united in the Neotropical aplocheiloids. In the generalized state (e.g., in *Rivulus*, fig. 13F) the branchiostegal rays are not conspicuous externally. Scales usually extend over this continuous covering of the ventral surface of the head which obscures the separation between the preoperculum and operculum.

There are no preopercular pores, which is concordant with the weakly developed or absent sensory canal in the preoperculum (fig. 13D). No Neotropical aplocheiloid examined has a complete canal in the preoperculum; although, there is a short canal in its dorsal extension in all except *Terranotus, Cynolebias, Campellolebias, Simpsonichthys, Cynopoecilus,* and *Leptolebias.* The canal is visible externally as an obsolescent canal, rather than as a pore or series of pores. Similarly, the dermosphenotic is reduced (fig. 17C) and carries just a small canal. In the Old World aplocheiloids, the dermosphenotic is more deeply concave. Also, as noted in the previous section, the lacrimal is a narrow and twisted bone in all aplocheiloids; it carries a distinct canal in the Old World aplocheiloids, whereas in those of the Neotropics, the canal is obsolescent.

As expected, a reduction in the sensory canal system in the opercular and infraorbital region is correlated with that on the dorsal surface of the head. The reduction involves the substitution of enclosed canals which open to the surface by pores for neuromasts or pit organs.

Gosline (1949) examined just one species of Neotropical aplocheiloid, *Rivulus holmiae,* and concluded that it had not developed supraorbital canals, or preopercular, mandibular, or preorbital canals. This was found to be true for all Neotropical aplocheiloids; however, there is not a progressive reduction of neuromast patterns within the group, but rather a further elaboration of the neuromast pattern in more derived genera.

The pattern of neuromasts is the simplest in primitive members of the genus *Rivulus.* For example, in *R. marmoratus,* there are four supraorbital neuromasts, which may correspond to the pores 1, 2a, 2b, and 5 or 6 of the general pattern.

The lacrimal, mandibular and preorbital pores typically are represented by neuromasts. The neuromast pattern is progressively more elaborate in the more derived species of *Rivulus* (e.g., *R. harti*) and in the other genera of Neotropical aplocheiloids. In a review of species of the nominal genera *Rachovia* and *Austrofundulus,* Taphorn and Thomerson (1978) illustrated a variety of neuromast patterns found among the species currently placed in those genera. There are a series of neuromasts running posteriorly from a position medial to the anterior naris and extending to the posterior limit of the orbit. The pattern continues in the preorbital region.

A derived form of this pattern is exhibited by members of the genus *Cynolebias* (fig. 13G, H, I). There are a series of minute neuromasts which resemble perforations of the skin. These neuromasts run posteriorly along the dorsal surface of the head from a position medial to the anterior naris to a position posterior to the orbit where the line turns abruptly back toward the orbit, then posteriorly again for a short distance, curving back to the path of the postorbital canal, continuing around the eye, and ending near the posterior naris.

A similar pattern is exhibited by some cyprinodontoids, e.g., the South American genus *Orestias* (fig. 14G, H, I) and the nominal Anatolian genus *Anatolichthys* and some species of *Aphanius.* This pattern is considered to be secondarily derived in the cyprinodontoids based on the fact that the last three mentioned genera share a series of derived characters with other cyprinodontiforms that are not shared by the aplocheiloids. The significance of the pattern exhibited by these genera will be evaluated in the discussion of their interrelationships.

The head squamation pattern of figure 14B is hypothesized to be primitive for cyprinodontiform fishes. Following the convention established by Hoedeman (1958), there is a single A scale, which is identified as the median scale lying posterior to a line drawn through the posterior limits of the orbits. It is preceded by two E scales, one of which overlaps the other. A single G scale precedes these, and there are often two or more F scales laterally.

The terminology of the head scales used to describe the general pattern found in cyprinodontiforms was not developed to describe this pattern, but for that typically found in *Rivulus* and other Neotropical aplocheiloids. Hoedeman considered the pattern of *Rivulus* (fig. 13B) to be a fundamental arrangement of head scales. The central A scale is surrounded by a series of scales which are coded B through E proceeding counterclockwise from the scale just posterior to A. This pattern is not fundamental for cyprinodontiforms, but is unique to the Neotropical genera. The unique component of the pattern in more derived species of *Rivulus* and the other Neotropical genera is the inclusion of the G scale in series surrounding the A, thus preventing the overlap of the E scales. Also, scales B through E are all approximately the same size, whereas, generally in cyprinodontiforms, the A, E, and G scales are prominent.

Hoedeman (1974) illustrated a pattern for *Cynopoecilus melanotaenia* in which there are two small G scales, rather than one, and these are not in series around the A. I have not observed this pattern in *C. melanotaenia,* and conclude that it is possibly part of intraspecific variation. There is a great deal of such variation with head squamation patterns. The single A scale is not always present, and when present can either overlie the circular arrangement of the B through E scales, or lie beneath them.

There are also a series of smaller scales anterior to the lettered scales, covering the dorsal surface of the head from a position over the middle of the eye to the margin of the frontals.

Taphorn and Thomerson (1978) reported much individual variation in the named scale patterns of Hoedeman and therefore questioned the value of this character to distinguish among species groups within the Neotropical aplocheiloids. Their judgment was borne out by this study, and it is concluded that the sensory neuromast patterns may be more readily characterized and incorporated into a phylogenetic analysis.

Lateral Ethmoid: Another series of characters uniting the Neotropical aplocheiloids into a monophyletic group concerns the relative shape and position of the lateral ethmoid and the vomer. The orientation and relative size of the lateral ethmoid varies among cyprinodontiforms, but the general condition among aplocheiloids is that exhibited by the Old World genus *Aphyosemion* (fig. 17A).

The vomer is broad and typically bears a patch of teeth. Its lateral processes extend anteriorly just under the lateral ethmoids. There is a distinct facet for articulation of the autopalatine on the anterior edge of the lateral ethmoid. This process, which is prominent in all species of *Profundulus* (fig. 57A), is not strongly formed in any other cyprinodontoids. It is considered to be a retained primitive character in *Profundulus.*

The medial face of the lateral ethmoid in Old World aplocheiloids is not expanded toward the parasphenoid. Within the Neotropical aplocheiloids, however, the medial processes of the lateral ethmoids are greatly expanded and lie just lateral or dorsal to the anterior arm of the parasphenoid (fig. 17C).

Maxilla: The maxilla among all aplocheiloids, *Profundulus* and fundulines is narrow and twisted (fig. 5B, C). The anterior arms of the maxilla in aplocheiloids and *Profundulus* extend medially toward the large rostral cartilage to which they are affixed by connective tissue fibers. In the Neotropical aplocheiloids alone, the arm has a process on its anterior face (fig. 5A), rather than being gently curved as in all other cyprinodontiforms with pronounced anterior arms.

### SUMMARY OF DERIVED CHARACTERS

1. First postcleithrum absent.
2. Branchiostegal and opercular membranes united.
3. Obsolescent preopercular and lacrimal canals.
4. Lacrimal, preopercular and mandibular canals represented by neuromasts.
5. Head scales arranged in circular pattern.
6. Medial process of lateral ethmoid expanded.
7. Process on ventral arm of maxilla.

RELATIONSHIPS OF NEOTROPICAL APLOCHEILOIDS: The interrelationships of Neotropical aplocheiloids have been discussed most recently by Weitzman and Wourms (1967) and Taphorn and Thomerson (1978). There are currently 13 nominal genera and subgenera in the group as listed above which together are defined as monophyletic by the characters just discussed.

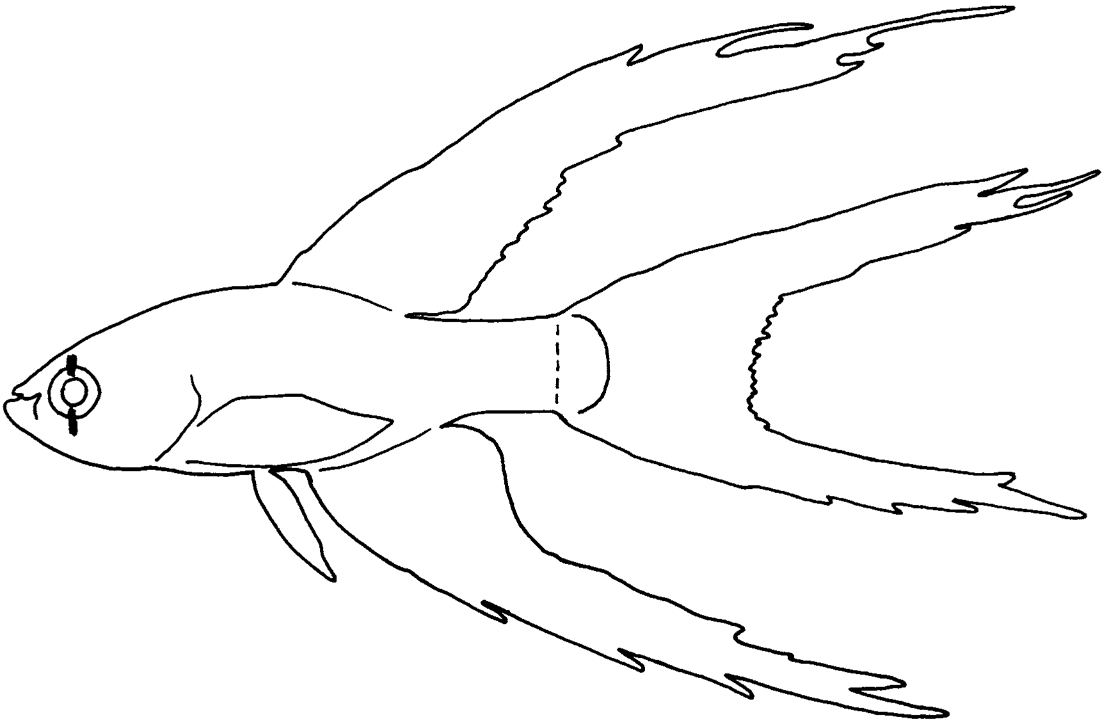

FIG. 19. Sketch of body form and fin formation in a male *Cynolebias* (*Austrofundulus*) *dolichopterus*. Dotted line approximates base of hypural plates. (After Weitzman and Wourms, 1967.)

Treatments of the interrelationships of these genera have focused on the overall similarity of genera without regard to the primitive or derived nature of characters, and, also, on the failure of current generic definitions to distinguish the included species from those of other genera. The latter problem is perhaps the most serious barrier to recognizing the monophyletic groups of species. Because no single character consistently distinguished all the species of *Pterolebias*, *Austrofundulus*, and *Rachovia*, Weitzman and Wourms suggested that they be included in one genus, although no formal taxonomic decisions were made. In the same paper, they described a new species of South American aplocheiloid which they hesitantly placed in the genus *Austrofundulus* on the basis of overall body shape and coloration. The species, *A. dolichopterus* (fig. 19) is readily distinguished from all other members of the group by its small size and extremely elongate fin rays. Taphorn and Thomerson removed *dolichopterus* from *Austrofundulus* and placed it in a new monotypic genus, *Terranotus*. They stressed that it had no clear relationship to any known genus, but that it might be more closely related to *Cynolebias* than to either *Austrofundulus* or *Rachovia*. The creation of monotypic genera for the reception of species whose placement in a taxonomic scheme is not readily apparent has been the trend in aplocheiloid systematics. Five of the 13 genera of Neotropical aplocheiloids are monotypic: *Terranotus*, *Simpsonichthys*, *Cynopoecilus*, *Campellolebias*, and *Trigonectes*.

Redefinitions of aplocheiloid genera based on derived characters rather than on unique combinations of characters will eliminate the ambiguous placement of species such as *dolichopterus*. The following phylogenetic analysis does not involve the revision of all species of the genera of Neotropical aplo-

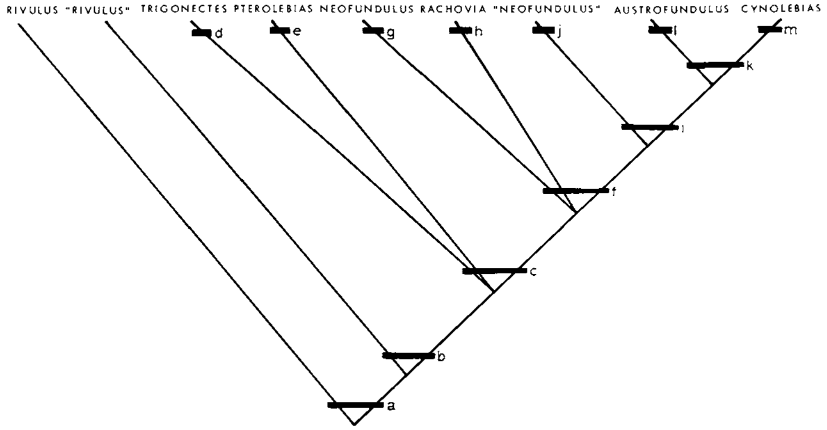

FIG. 20. Cladogram of relationships of Neotropical aplocheiloids. Node A: lack of the first postcleithrum; branchiostegal rays covered; reduced cephalic sensory pore pattern; reduced dermosphenotic; reduced lacrimal; reduced preopercular; medial processes of the lateral ethmoids expanded; vomer triangular posteriorly; maxilla with anterior process; Node B: cartilaginous interhyal; pelvic fin rays seven or more; Node C: elongate rostral cartilage; extension of the pectoral fin rays to the base of the pelvics; Node D: reduction of anterior ramus of the alveolar arm; derived pigmentation pattern; Node E: lack of the interarcual cartilage; Node F: vertical bar through the eye; thickened anal rays in females; tendency to develop a fatty predorsal ridge in older males; Node G: derived color pattern; Node H: reduced number of scales in lateral series; Node I: dorsal fin rays number 14 or more; Node J: no derived characters; Node K: first proximal radial absent; enlarged spine on first vertebra; reduced fourth ceratobranchial dentition; Node L: pigmented anal papilla; Node M: caudal fin not scaled; preopercular canal closed.

cheiloids which comprise over 110 species (Lazara, 1979). Instead, interrelationships based primarily on the type species of nominal genera are estimated to produce a working model of the phylogeny of this group as in the cladogram of figure 20. No new generic names are proposed for species excluded from nominal genera, since it is believed that new generic names should be proposed only for definable monophyletic groups of species.

*Rivulus* currently contains over 60 species and as such is the largest genus within the group. Traditionally it has been defined on the basis of the presence of a caudal ocellus in females (fig. 54). The presence of such an ocellus in females of the African genus *Aphyosemion* suggests that this character is primitive for all aplocheiloid fishes.

Annualism: Among the Neotropical aplocheiloids, only the species of the genus *Rivulus*, except for *R. stellifer* Thomerson and Turner, are reportedly nonannual. *Rivulus stellifer*, in this scheme, is hypothesized to be more closely related to the more derived genera of Neotropical aplocheiloids. The nature of the development of many species of *Rivulus* is unknown, and there are probably more annual species included. Furthermore, the annualism of the nominal genera *Trigonectes* and *Rivulichthys* is merely inferred by their locality of capture. Thus, it has not been determined whether the annual Neotropical aplocheiloids form a monophyletic group. This possibility remains to be tested by a revision of the nominal species of *Rivulus* in light of the present findings.

Jaw Structure: All Neotropical aplocheiloids excluding the species of *Rivulus* examined, have an elongate rostral cartilage (fig. 4) extending for at least half its length beyond the tips of the premaxillary ascending processes. The primitive state of the rostral cartilage for cyprinodontiforms as evidenced by its occurrence in all other aplocheiloids, and in a slightly modified state in *Profundulus*, is as a pentagonal block of cartilage, the posterior end of which extends just slightly beyond the tips of the ascending processes (e.g., in *R. harti,* fig. 5A).

The monotypic *Trigonectes* and its included species *strigabundus* and the genus *Rivulichthys* are distinguished from all other aplocheiloids by their sharply angled mouth cleft. This is produced by a foreshortening of the anterior ramus of the arm of the premaxilla (fig. 21). Such an oblique cleft and reduction of the anterior ramus also occur in a nominal species of *Rivulus, R. rogoaguae,* considered herein to be a close relative of *strigabundus* and *rondoni.*

Coloration: Species of *Trigonectes* and *Rivulichthys,* as well as *R. rogoaguae,* also have a derived color pattern consisting of four rows of brown or red reticulations along the sides of the body. The dorsal, anal, caudal, and pectoral fins also have two or three rows of reticulations.

A similar color pattern occurs in one other species of South American aplocheiloids, *Neofundulus paraguayensis. Neofundulus paraguayensis* on the basis of other characters, which will be discussed, is apparently not closely related to *strigabundus* and *rondoni. Rivulus rogoaguae,* on the other hand, most likely belongs in a monophyletic group with *strigabundus* and *rondoni,* although it is considered to be a synonym of neither.

A vertical bar through the eye is a prominent component of the color pattern of species of the genera *Rachovia, Austrofundulus, Cynolebias,* as well as its included subgenera, and the genus *Neofundulus* (fig. 19). This bar is not present in species of *Pterolebias, Rivulichthys, Trigonectes,* nor any species of *Rivulus* examined. A bar occurs in just one other species of aplocheiloids, *Nothobranchius microlepis* of Somalia. The occurrence of such a derived pattern in what have otherwise been evaluated as two unrelated groups of aplocheiloids suggests that this pattern has been independently derived twice within the aplocheiloids.

The two species of *Austrofundulus, A. limnaeus* and *transilis,* are distinguished from all other Neotropical aplocheiloids by having heavily pigmented anal papillae. The anal papillae are only slightly pigmented or bare in other genera.

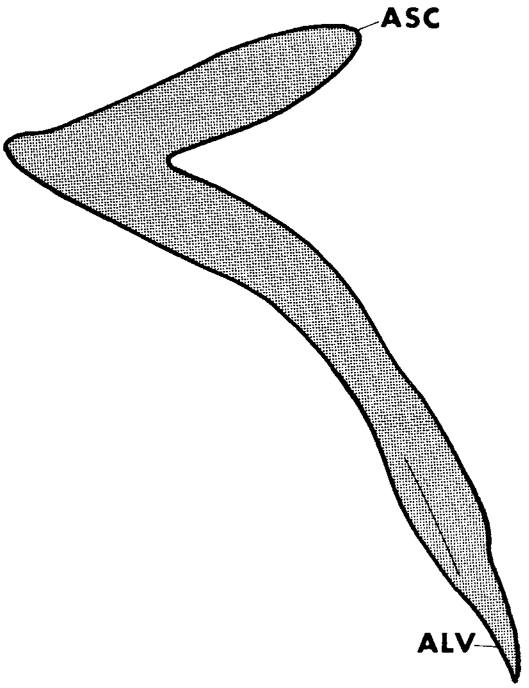

FIG. 21. Diagrammatic representation of premaxilla of *Trigonectes* (*Rivulichthys*) *rondoni,* lateral view.

Predorsal Ridge: Taphorn and Thomerson (1978) stated that only members of the genera *Rachovia* and *Austrofundulus* as they defined them, developed a fatty predorsal ridge, and that this ridge did not develop in *Terranotus.* However, in all male *Terranotus* examined, including types, a prominent dorsal ridge was found comparable to those in *Rachovia* and *Austrofundulus.* Therefore, it is proposed that this character is derived for this inclusive group.

Spine on First Vertebra: The inferred more primitive genera, including *Rachovia, Pterolebias, Trigonectes, Rivulichthys,* and *Rivulus,* have a relatively short spine on the first vertebra and a correspondingly straighter dorsal profile than in *Austrofundulus, Terranotus* and *Cynolebias.* In these latter genera, the dorsal profile is greatly arched (figs.

13G, 19), apparently as a result of an enlarged spine on the first vertebra.

Gill Arches: The species of the genus *Rivulus* may be divided into two groups. One includes the smaller forms such as *cylindraceus, marmoratus,* and *heyei.* These are all characterized by having an interhyal which is ossified; that is, there is a perichondrally ossified element between the posterior ceratohyal and hyomandibula. This is the condition typical of the interhyal of teleost fishes. The larger species of *Rivulus,* of which *harti* may be considered typical, have an unossified interhyal instead. The character of an unossified interhyal, however, does not define a monophyletic group of *Rivulus* species, for it is found in all species examined of all remaining Neotropical aplocheiloids. Thus, it indicates that some species of *Rivulus* are more closely related to the other genera than to some species of *Rivulus.* Hence, the genus as currently defined is paraphyletic.

*Rachovia* has fourth ceratobranchials which are covered with teeth. In *Austrofundulus* and *Terranotus,* there are no teeth on the medial expansion of the gill arch elements, but the posterior arm does possess at least one tooth. In *Cynolebias,* the fourth ceratobranchials are devoid of teeth. Therefore, the reduction of teeth on the fourth ceratobranchial is assessed as a defining character of a group including *Cynolebias, Austrofundulus,* and *Terranotus.*

All characters could not be determined for the sole specimens of *ornatipinnis* and *paraguayensis* studied; however, they do have the primitive character of fourth ceratobranchials covered with teeth.

The interarcual cartilage is present primitively in the aplocheiloids (e.g., as in *Austrofundulus transilis,* fig. 6A) and in all Neotropical aplocheiloids except those of the nominal genus *Pterolebias,* in which it is absent. The cartilage is reduced in one species of *Rachovia, R. maculipinnis.*

Fins: All species of *Rivulus* examined (except *rogoaguae*) have all fins rounded. There are never any caudal, pelvic, dorsal or anal fin extensions as found in the other Neotropical aplocheiloids. Typically, the pectoral fins are elongate and reach the base of the pelvic fins in *rogoaguae* and all non-*Rivulus* species. *Cynolebias* and its relatives have a caudal which is rounded as a result of a unique orientation of the procurrent rays perpendicular to the vertebral column.

There are usually six pelvic fin rays in atherinomorph fishes. There are six in all Old World aplocheiloids as well as members of the genus *Rivulus* with an ossified interhyal (e.g., *R. marmoratus*). In the larger species of *Rivulus* examined, e.g., *harti* and *stellifer,* the number of pelvic fin rays is increased to seven or eight as it is in all other Neotropical aplocheiloids. This increase is interpreted as a derived character at this level. The pelvic fin rays rarely are increased to seven among the cyprinodontoids in some species of the North American cyprinodontines.

The nominal species of *Cynolebias* and *Terranotus* lack scales on the caudal fin. As mentioned, the scaled caudal fin is apparently primitive for aplocheiloids, and is present in all other members.

Taphorn and Thomerson suggested that *Terranotus* may be more closely related to *Cynolebias* because its anterior proximal anal radials "articulate" with ribs rather than hemal spines. However, within actinopterygian fishes, the proximal anal radials never properly articulate with either ribs or hemal spines, but are often found intercalated with the latter. The character to which Taphorn and Thomerson referred could more appropriately be described in terms of the position of the anal fin relative to the abdominal and precaudal vertebrae.

In *dolichopterus,* there are 14 abdominal vertebrae and 12 precaudal; the first proximal anal radial (equivalent to the second of *Rivulus* since the first is lost) extends between the pectoral ribs of the ninth abdominal vertebra.

In the one species of *Pterolebias* which exhibits this character, there are 15 abdominal vertebrae, 18 precaudal, and the first proximal anal radial extends just behind the ribs of the twelfth abdominal.

Among species of *Cynolebias,* the vertebral number is quite variable. In *C. melano-*

*taenia,* there are 12 abdominal, 17 precaudal, and the first proximal anal radial extends just posterior to the ribs of the tenth abdominal vertebra. In *C. whitei,* the counts are 14 plus 15, with the anal radial at the rib of the eighth abdominal. In *C. elongatus,* the counts are 16 plus 21, with the anal radial at the rib of the fourteenth abdominal.

Perhaps a derived character is the extreme anterior position of the anal fin which would indicate that *dolichopterus* is closely related to a group of *Cynolebias* species that includes *whitei.* However, in addition to contradicting the derived characters of *Cynolebias* not shared by *dolichopterus,* it conflicts with another character that may be of significance in *Cynolebias* interrelationships; that is, the number of anal fin rays. In both *elongatus* and *whitei* there are more than 20; in *dolichopterus* they range from 15 to 18 (Weitzman and Wourms, 1967). The usefulness of this character can only be determined by a survey of its states among all species of *Cynolebias.*

The genus *Neofundulus* currently contains two species, *paraguayensis* Myers, the type, and *ornatipinnis* Myers. Both species are known from only a few specimens, and only the holotype of each has been examined as part of this study.

Arambaru, Arambaru, and Ringuelit (in de Souza, 1979) suggested the two species be synonymized. This is opposed by evidence that they are not even closest relatives. De Souza (1979) reported meristic data for a recent collection of *paraguayensis,* and listed these along with values for the holotypes of each species. The number of dorsal fin rays in *paraguayensis* ranges from 10 to 13; in *ornatipinnis* it is 15. The number of anal rays is 12 to 16, and 18, respectively. The number of scales in the lateral series ranges from 34 to 38 in *paraguayensis,* and is 37 in *ornatipinnis.*

The holotype of *paraguayensis* is a female, and that of *ornatipinnis* a male. Therefore, from the type material alone, it is difficult to tell whether the differences are due to sexual dimorphism alone. (In a group of species in the genus *Cynolebias,* males have higher dorsal and anal fin ray numbers.)

However, de Souza (1979) reported meristic data for what were referred to as nine randomly chosen individuals of *paraguayensis,* that included two juveniles. The holotype is a female, and it can reasonably be assumed that at least one of the nine specimens was a male; therefore, I conclude that *ornatipinnis* and *paraguayensis* are two species which may be easily distinguished on the basis of meristic characters.

Furthermore, the disparate meristic data indicate the nonmonophyletic nature of the genus. Taphorn and Thomerson separated *Rachovia* from *Austrofundulus* the basis of, among other characters, fewer dorsal fin rays which are generally less than 13 (range 9–14) in *Rachovia,* as compared with generally 14 or more (range 12–18) in *Austrofundulus.* Although there is range overlap, the increase in dorsal fin ray numbers in *Austrofundulus* and *N. ornatipinnis* is consistent with an increase in dorsal fin ray numbers to 15 or more in *Cynolebias* and *Terranotus.*

The first proximal anal radial is often fused to the second at its base. Nonetheless it is present in the genus *Rachovia,* as well as in the other more primitive Neotropical genera. The radial is absent (fig. 22) in the genus *Austrofundulus* as well as in *Terranotus* and *Cynolebias* and its included subgenera.

Scales in a Lateral Series: The Neotropical aplocheiloids typically have a high number of scales in a lateral series. Determining the polarity of scale number, however, presents certain problems since the scale count is not high in all members. Within primitive members of the group, such as *R. marmoratus,* the scale count is over 40, greater than the more typical number of 30 for cyprinodontiforms as a group. The scale count is high also in some members of the derived genus *Cynolebias,* such as *C. elongatus,* in which the scales number over 60. There are members of the genus *Cynolebias* which have lower counts in the thirties and forties. Among all Neotropical aplocheiloids, however, the count is low only in members of the genus *Rachovia,* as the genus is delimited by Taphorn and Thomerson. In fact, they gave as a defining character of the genus a lateral series scale count of less than 32,

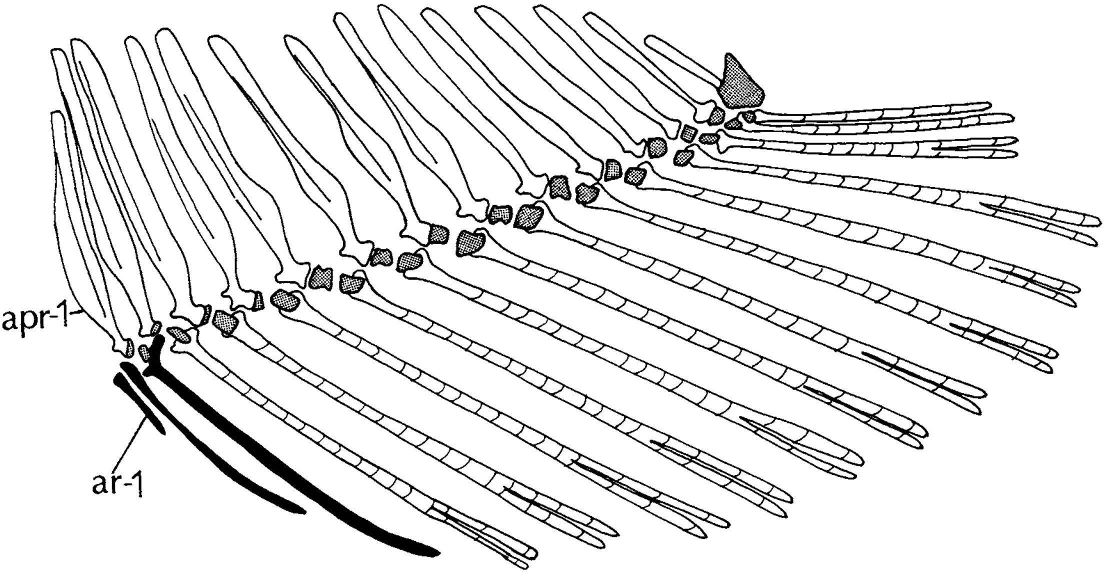

FIG. 22. Diagrammatic representation of anal fin of *Austrofundulus transilis*. Unbranched anal rays are blackened, middle and distal anal radials are stippled.

lower than any other Neotropical aplocheiloid. Taking all other characters into consideration, the high scale count is derived for some group, the limits of which cannot be readily determined at the level of this study. Therefore, it is logical to conclude that the reduced scale count of *Rachovia* is a derived character, or else the increased number of scales has occurred several times which is an unparsimonious assessment of this character.

SUBGROUP DEFINITION AND COMPOSITION: The assignment of species currently in the genus *Rivulus* to one group or another requires examination of all species for the state of the interhyal and number of pelvic rays. Such a survey is out of the scope of the present study. *Rivulus cylindraceus* is the type species of the genus; therefore, it will retain the name. This leaves those species of *Rivulus* with a cartilaginous interhyal without a name. I suggest they be referred to as "*Rivulus*" rather than propose a new name at this time since the relationship of all species of "*Rivulus*" to the remaining Neotropical genera is uncertain, as is, therefore, the monophyly of the genus.

The species of *Rivulichthys*, *Trigonectes strigabundus*, and *Rivulus rogoaguae* share a pointed snout (caused by reduction of the anterior ramus of the premaxilla) and a derived color pattern. I propose, therefore, that the two genera and *R. rogoaguae* be grouped in *Trigonectes*, of which *Rivulichthys* is a junior synonym.

The nominal genus *Neofundulus* is considered to contain one species *paraguayensis*. The band of pigment on the ventral edge of the caudal fin in males is a character it shares with *Rachovia*. However, this character may very well be part of a transition series from the pigmentation pattern derived for aplocheiloid fishes; that is, a band of white or yellow pigment on both dorsal and ventral margins of the caudal. Therefore, although *Rachovia* and *Neofundulus* are considered to be included in a monophyletic group with *Austrofundulus*, *Terranotus*, and *Cynolebias*, this relationship is represented as an unresolved trichotomy (fig. 20).

*Neofundulus ornatipinnis* does not have the pigmentation pattern, yet, as stated, has an elongate dorsal fin. The condition of the holotype precludes its inclusion in any of the recognized genera. Therefore, I propose that it be referred to as "*Neofundulus*" *ornatipinnis* until additional specimens are available.

Six nominal species have been described in the genus *Pterolebias*: *longipinnis* Garman, *zonatus* Myers, *peruensis* Myers, *bockermanni* Travassos, *hoignei* Thomerson, and *maculipinnis* (Weibezahn). They all possess a dorsal fin of 10 to 12 rays which is set back on the body, normally the first ray being over the second half of the anal fin; the caudal fin is finely scaled for at least one-third its length; and, the caudal peduncle is strongly compressed laterally. These characters, however, are typical for all species of Neotropical aplocheiloids discussed so far, or, as in the case of the compressed caudal peduncle, may be an artifact of preservation (Weitzman and Wourms, 1967). As such, the genus has never been defined as a monophyletic group. Taphorn and Thomerson (1978) removed *maculipinnis* from *Pterolebias* and placed it in the genus *Rachovia*, after Thomerson (1974) stated that three species (*bockermanni, maculipinnis,* and *peruensis*) are probably not closely related to the other members of *Pterolebias*. The removal of *maculipinnis* from a close relationship to *longipinnis* seems to be a valid decision based on the following characters:

*Pterolebias longipinnis* and *zonatus* both lack the interarcual cartilage, a lack that may be considered a defining character of *Pterolebias*. This element is present in *maculipinnis*, although apparently reduced relative to the generalized state for aplocheiloids as previously discussed.

The species *maculipinnis* shares with the remaining Neotropical aplocheiloids (species assigned to *Rachovia, Austrofundulus, Terranotus, Neofundulus,* and *Cynolebias*): a vertical bar running from below the eye to near the dorsal surface of the head; thickened anal rays in females; and the tendency of males to develop a fatty predorsal ridge.

Provisionally, *Rachovia* may remain as delimited by Taphorn and Thomerson; however, the four included species *brevis, maculipinnis, pyropunctata,* and *hummelincki* might not constitute a monophyletic group. They are distinguished from other Neotropical aplocheiloids with a vertical bar through the eye and a fourth ceratobranchial covered by teeth by having a lateral series scale count of less than 32 (Taphorn and Thomerson, 1978). *Terranotus*, with an unscaled caudal fin and a closed preopercular canal, is hypothesized to be the sister group of an assemblage of four genera: *Cynolebias, Simpsonichthys, Cynopoecilus,* and *Campellolebias*. The members of these four genera all possess rounded caudal fins in both sexes and have fourth ceratobranchials without teeth. They all have been suggested as synonyms at one time or another (Myers, 1942; Lazara, 1979), and on the basis of their shared characters, I unite them (along with *Terranotus*) within their senior synonym, *Cynolebias*.

CLADISTIC SUMMARY OF NEOTROPICAL APLOCHEILOIDS: *Rivulus* and other Neotropical aplocheiloids share the derived characters outlined in the previous section: absence of a first postcleithrum; a unique head squamation pattern; the uniting of the opercular and branchiostegal membranes; reduction of the preopercular and dermosphenotic canals; the medial expansion of the lateral ethmoids and posterior extension of the vomer; and, the triangular process on the anterior face of the medial arms of the maxilla.

The genus *Rivulus* is paraphyletic, and its species are referenced to two genera *Rivulus* and "*Rivulus*."

Members of "*Rivulus*" share with other Neotropical aplocheiloids, excluding *Rivulus*, a cartilaginous interhyal and seven or more pelvic fin rays. In addition, all species in the genus *Rivulus* are nonannual, whereas at least one of the genus "*Rivulus*," *stellifer* Thomerson and Turner (1973), is annual.

"*Rivulus*" and *Rivulus* are excluded from a larger group which is defined by an elongate rostral cartilage, and extensions of the pectoral fin rays to the base of the pelvics. Within this larger group, three subgroups are recognized:

1. *Trigonectes*, of which *Rivulichthys* is considered to be a junior synonym, is defined by an oblique mouth cleft formed prin-

cipally by the reduction of the anterior ramus of the premaxilla.

2. *Pterolebias* is defined here by its lack of the interarcual cartilage.

3. A group including *Rachovia, Neofundulus, Austrofundulus, Terranotus* and *Cynolebias* is defined by the following characters: a vertical bar through the eye often extending on to the top of the head; thickened anal rays in females; and the tendency to develop a fatty predorsal ridge in older males. *Rachovia* may not be definable as a monophyletic group, but is retained here to reference its four included species which may be distinguished from other members of group 3 that have teeth on the fourth ceratobranchial by its low number of scales in a lateral series.

As presently defined, *Neofundulus* is polyphyletic. *Neofundulus ornatipinnis* is considered to be more closely related to the more derived aplocheiloids *Cynolebias, Austrofundulus,* and *Terranotus* on the basis of its increase in dorsal fin rays. It is the sole constituent of the genus "*Neofundulus*."

*Terranotus, Austrofundulus,* and *Cynolebias* lack the first proximal anal radial; have a large spine on the first vertebra; and have reduced dentition on the fourth ceratobranchial.

*Austrofundulus* is defined by its darkly pigmented anal papilla.

*Terranotus* and *Cynolebias* have a caudal fin which is not finely scaled and lack a preopercular canal. A group of species has a unique head neuromast pattern and an increase in the number of dorsal and anal fin rays in males. These two characters define subgroups of *Cynolebias*. Since there is no longer reason to maintain *Terranotus* as a monotypic genus, I propose that this genus be considered synonymous with *Cynolebias*.

## OLD WORLD APLOCHEILOIDS

Members of the aplocheiloids of the Old World have often been referred to as the most primitive of all cyprinodontiforms. Myers (1958) stated that the genus *Aplocheilus* represents the most basic characteristics of cyprinodontiform fishes which have either been lost or become more derived in other genera. These characters include the arm of the premaxilla being free rather than embedded in the skin on the side of the head, and the swimbladder extending through several hemal arches rather than ending at the first hemal arch. My own analysis of derived characters of the aplocheiloids and of those which define the Old World aplocheiloids, indicates that *Aplocheilus* is a relatively derived aplocheiloid genus.

Aplocheiloids of the Old World are currently classified in 29 nominal genera and subgenera. These include *Aplocheilus* of the Indian subcontinent and Laurasia extending along the Indo-Australian archipelago to Java; *Pachypanchax* of Madagascar and the Seychelles; and the African genera *Epiplatys* and four proposed subgenera; *Aphyosemion* and 11 subgenera; *Adamas*; *Nothobranchius* and four included subgenera; and *Fundulosoma* (fig. 23). Together they comprise nearly 300 species, over 100 of which are referred to the genus *Aphyosemion* or one of its subgenera.

The definition of the Old World aplocheiloids as a monophyletic group again supports the contention that annualism is a lifestyle which has either arisen at least twice within cyprinodontiform fishes, or is a characteristic that in some sense is basic to all members.

CHARACTER ANALYSIS: Shoulder Girdle: The Old World aplocheiloids are distinguished from all other killifishes by the fusion of the posttemporal and supracleithrum (fig. 7C) to form one slender bone connecting the shoulder girdle to the skull. The fusion is complete, and no joint lines are visible. In the Neotropical aplocheiloids, the posttemporal and supracleithrum are similarly shaped, however, the two bones may always be separated easily.

Gill Arches: Two derived characters of the gill arches distinguish the Old World aplocheiloids. One is the reduction of the basihyal to a small triangular-shaped bone which is capped by a large cartilaginous wedge (fig. 11A). As stated, in all aplocheiloids, the basihyal is very wide, and forms the basis of a wide "tongue" which is visible upon opening

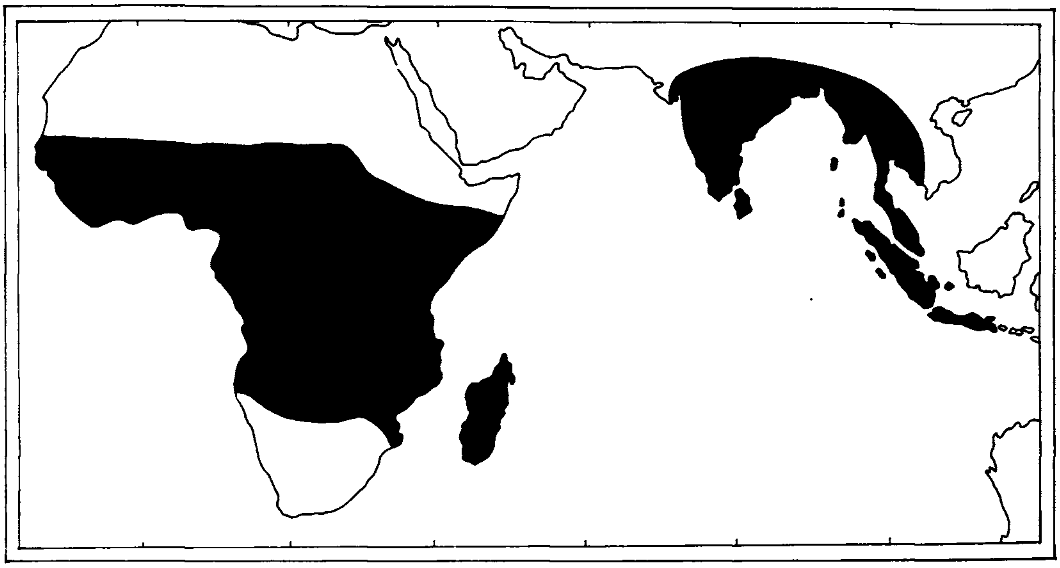

FIG. 23. Distributional limits of Old World aplocheiloids.

the mouth. In the Neotropical aplocheiloids, as well as in the cyprinodontoids and other atherinomorphs, the basihyal is ossified for more than half its length.

A second character concerns the attachment of the interarcual cartilage to the second pharyngobranchial. The Neotropical aplocheiloids exhibit the primitive state for cyprinodontiforms; that is, the cartilage attaches to a small flange of bone lateral to the cartilaginous extension of the pharyngobranchial (fig. 6A) as it does in the aplocheiloids.

In the Old World aplocheiloids, the cartilage attaches in the same position, but the bony flange is absent; thus, the cartilage nearly abuts the cartilaginous articulation point of the pharyngobranchial (fig. 24A).

In the genus *Nothobranchius*, the cartilage attaches directly to the cartilaginous head of the pharyngobranchial (fig. 24B). This character is apomorphic for the genus.

Premaxillary: The premaxillary ascending processes are flat and broad in the Neotropical aplocheiloids and in *Profundulus*. This state is most parsimoniously assessed as the most primitive among cyprinodontiforms as discussed in the section on derived characters of the group.

Within the Old World aplocheiloids, the premaxillary ascending processes are tapered posteriorly to form, in the most derived state, the greatly expanded triangular processes of *Aplocheilus* (fig. 4A). In *Pachypanchax* (fig. 4B) and *Epiplatys* and its included subgenera, the processes are also expanded, although not to the degree exhibited by *Aplocheilus*.

In *Aphyosemion* (fig. 4C), *Nothobranchius* and *Fundulosoma*, the processes are tapered posteriorly, but never as widely expanded as in any of the three above mentioned genera.

### SUMMARY OF DERIVED CHARACTERS

1. Supracleithrum fused to posttemporal.
2. Small, triangular basihyal capped by a wedge of cartilage.
3. Interarcual cartilage attached directly to lateral face of the second pharyngobranchial.
4. Premaxillary ascending processes tapered.

RELATIONSHIPS OF OLD WORLD APPLOCHEILOIDS: The Old World aplocheiloids, like the Neotropical aplocheiloids,

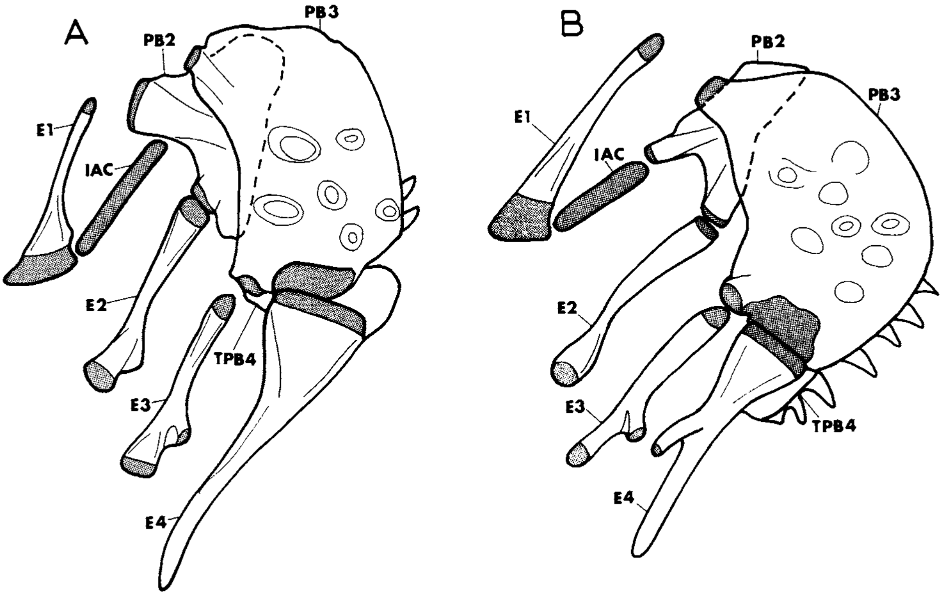

FIG. 24. Diagrammatic representation of dorsal view of dorsal gill arches of A. *Aplocheilus panchax*, B. *Nothobranchius melanospilus*. Cartilage is stippled.

have been treated as a natural group of fishes (e.g., Scheel, 1968) although their monophyly had never been tested. In addition to considering *Aplocheilus* as the most primitive cyprinodontiform (e.g., Myers, 1958), various authors suggest that the annual Old World aplocheiloids are the closest relatives of the Neotropical aplocheiloids.

Furthermore, the Old World aplocheiloids were considered by many workers to be closely related to the procatopines, the other group of cyprinodontiforms which inhabits subsaharan Africa. Ahl (1924, 1928), for example, grouped the two without questioning their monophyly; more recently, Huber (1979) described a new genus and species, *Adamas formosus,* which he considered to be intermediate between Old World aplocheiloids of the genus *Aphyosemion* and the procatopines. Such conclusions were a product of the ambiguous definitions previously put forth for the subfamilies Rivulinae and Aplocheilichthyinae. Nevertheless, as understood here, these two distributionally similar groups have little more than primitive characters in common.

The procatopines do not possess any of the derived characters of Old World aplocheiloids summarized above; they possess only one of the derived characters for aplocheiloids as a whole, the cartilaginous mesethmoid. This condition is considered to be independently derived in these two groups, as well as in Anatolian cyprinodonts.

Procatopines, however, do share a series of unique features with the rest of the cyprinodontoids. Thus, procatopines and aplocheiloids are not considered together further.

Taxonomic revisions of Old World aplocheiloids, like those of New World forms, place emphasis on the recognition of differences among taxa rather than on the discovery and description of derived characters shared among taxa. Emphasis on differences has led to the naming of four subgenera of *Epiplatys,* four subgenera of *Nothobranchius,* and the division of *Aphyosemion* into 13 genera and subgenera.

In a recent paper by Radda (1977), four new subgenera are named, each to encompass a group of species referable to *Aphyosemion.* Radda included a phylogenetic tree which purports to summarize the relationships of subgenera within the genus. The monophyly of *Aphyosemion* is doubtful, following Radda's diagram, for the subgenus *Pronothobranchius* and the genus *Fundulosoma,* considered here as close relatives, are included as more closely related to some subgenera of *Aphyosemion* than they are to each other. Furthermore, the genus *Nothobranchius* is not considered at all; therefore, it is unclear whether the implication is that *Nothobranchius* is in turn most closely related to *Fundulosoma* or *Pronothobranchius,* to some subgroup of *Aphyosemion,* or whether it need be considered at all in a revision of *Aphyosemion.*

The genus *Aphyosemion* is large, currently comprising over 110 species; if some members are more closely related to *Nothobranchius* species then the two genera must be considered together in a phylogenetic analysis. If the two genera do not form a monophyletic group, then *Nothobranchius* need not be considered in a study of the interrelationships of *Aphyosemion* and its subgenera. The problem of defining monophyletic genera and subgenera extends to all members of the Old World aplocheiloids. Scheel (1972) has recommended that the genera *Epiplatys* and *Aplocheilus* be synonymized. Clausen (1967) has named a new subgenus of *Epiplatys* to included the species *E. duboisi*; a subgenus *Aphyoplatys* is named to indicate that this species is intermediate between *Aphyosemion* and *Epiplatys.* Wildekamp (1977) has recently named a new subgenus of *Nothobranchius* to include the species *N. janpapi*; it is named *Aphyobranchius* to reflect its intermediacy between *Aphyosemion* and *Nothobranchius.*

It is of little use, however, to know that all the nominal genera of Old World aplocheiloids grade into one another from the *Aplocheilus* type to the *Nothobranchius* type. Logically, there is no reason not to classify all the species in one genus; however, that too would be avoiding the problem of the interrelationships of the included species as much as if each species were put into its own genus. Unambiguous definitions of monophyletic groups of nominal genera would allow for the reference of a particular species to one monophyletic group or another, and avoid the confusion created by the current generic limits. For example, *Aphyobranchius janpapi* is either more closely related to species of *Nothobranchius* or to some group of *Aphyosemion.* A concise definition of each group would allow such a decision to be made.

As for the Neotropical aplocheiloids, this analysis does not include the revision of all species of each genus. Rather, it is an attempt to identify and define on the basis of shared derived characters the major monophyletic groups of species and their proposed interrelationships (given in the cladogram of fig. 25) which will eventually lead to the definition of monophyletic genera.

Supraspecific categories of Old World aplocheiloids may be divided into two major monophyletic groups. One is referred to as the *Aphyosemion-Nothobranchius* group; and the second is referred to as the *Aplocheilus-Pachypanchax-Epiplatys* group. The interrelationships of the members of the two are discussed separately with reference to the states of characters in the other, in the Neotropical aplocheiloids, and in cyprinodontiforms as a whole.

### THE *Aphyosemion-Nothobranchius* GROUP

Species in this group are currently classified in four genera and fifteen subgenera. These are *Aphyosemion* Myers with eleven subgenera: *Archiaphyosemion* Radda, *Mesoaphyosemion* Radda, *Kathetys* Huber, *Fundulopanchax* Myers, *Paludopanchax* Radda, *Chromaphyosemion* Radda, *Callopanchax* Myers, *Raddaella* Huber, *Diapteron* Huber and Seegers, *Paraphyosemion* Kottelat and *Gularopanchax* Radda; *Nothobranchius* Peters, with four subgenera: *Adiniops* Myers, *Pronothobranchius* Radda, *Zonothobranchius* Radda, and *Aphyobranchius* Wildekamp; and *Fundulosoma* Ahl and *Adamas* Huber, two monotypic genera.

Most of these names are unfamiliar to the majority of workers on cyprinodontiform fishes since nearly all have been just recently described in journals that are not widely dis-

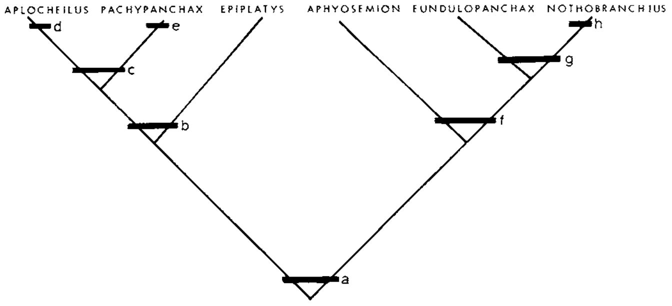

FIG. 25. Cladogram of relationships of Old World aplocheiloids. Taxa treated as subgenera not included in diagram (see text for further information). Node A: posttemporal fused to supracleithrum; reduction of basihyal to small, triangular wedge; interarcual cartilage attached to second pharyngobranchial which lacks a bony flange; premaxillary processes tapered posteriorly; Node B: broad, flattened upper jaw caused by expanded premaxillary ascending processes; expanded coronoid process on the dentary; bifurcate upper hypural plate in juveniles and some adults; loss of the uncinate process on fourth epibranchial; Node C: lower limb of posttemporal represented by ligament; teeth on third and fourth hypobranchials; dorsal ocellus in females; orbital rim attached only ventrally; darkened caudal fin margin; Node D: premaxillary ascending processes expanded medially and overlapping in the midline; attenuate lower jaw; Node E: hypural fan in adults; lateral scales of male angled away from body; Node F; bifid epipleural ribs; reduced chromosome number; attenuate posterior extension of the vomer; Node G: dorsal fin rays fourteen or more; dorsal origin opposite anal origin; swimbladder not expanded past first arch; Node H: preopercular canal open, not represented by pores; attachment of the interarcual cartilage directly to the second pharyngobranchial; oval eggs.

tributed publicly. Nonetheless, they represent available supraspecific categories within the *Aphyosemion-Nothobranchius* group; therefore, their references are summarized in the systematic accounts, and they are considered herein.

CHARACTER ANALYSIS: Bifid Epipleural Ribs: Bifid epipleural ribs have been used to distinguish species of the genus *Aphyosemion* from those of the genus *Nothobranchius*. Typically, in *Aphyosemion*, the first five or six epipleural ribs are strongly bifid distally (fig. 26). This derived character is unambiguously present in all species of *Aphyosemion* examined, including *A. petersi*, a species which has alternately been placed in the genus *Aphyosemion*, and in *Epiplatys*. On this basis, *petersi* should properly be placed in the *Aphyosemion-Nothobranchius* group.

In some species of *Aphyosemion*, for example, *A. gulare* and *sjoestedti*, and in *Nothobranchius*, the epipleural ribs are often not as strongly bifid as in most of the species of *Aphyosemion*; however, on close examination, they are easily determined as bifid. For example, in *Nothobranchius orthonotus*, the type of the genus, the first six epipleural ribs are unambiguously bifid. This character does not appear to be related to the size or age of specimens, nor is any sexual dimorphism apparent.

Vomer: The vomer typically has a broad posterior extension in cyprinodontiform fishes (e.g., in *Aplocheilus panchax*, fig. 17B). In contrast, in members of the *Aphyosemion-Nothobranchius* group the posterior extension of the vomer is narrow (fig. 17A). This sets off the anterior extension of the vomer as a large rectangular element.

Chromosome Number: Fishes of this group exhibit some of the lowest chromosome numbers known for teleost fishes. Teleosts generally have a haploid chromosome number of 24, and therefore a diploid number of 48. Gyldenholm and Scheel (1971) listed haploid and diploid chromosome numbers of temperate and tropical freshwater fishes in 19 families. Included were representatives of the percomorph, ostariophysan, atherino-

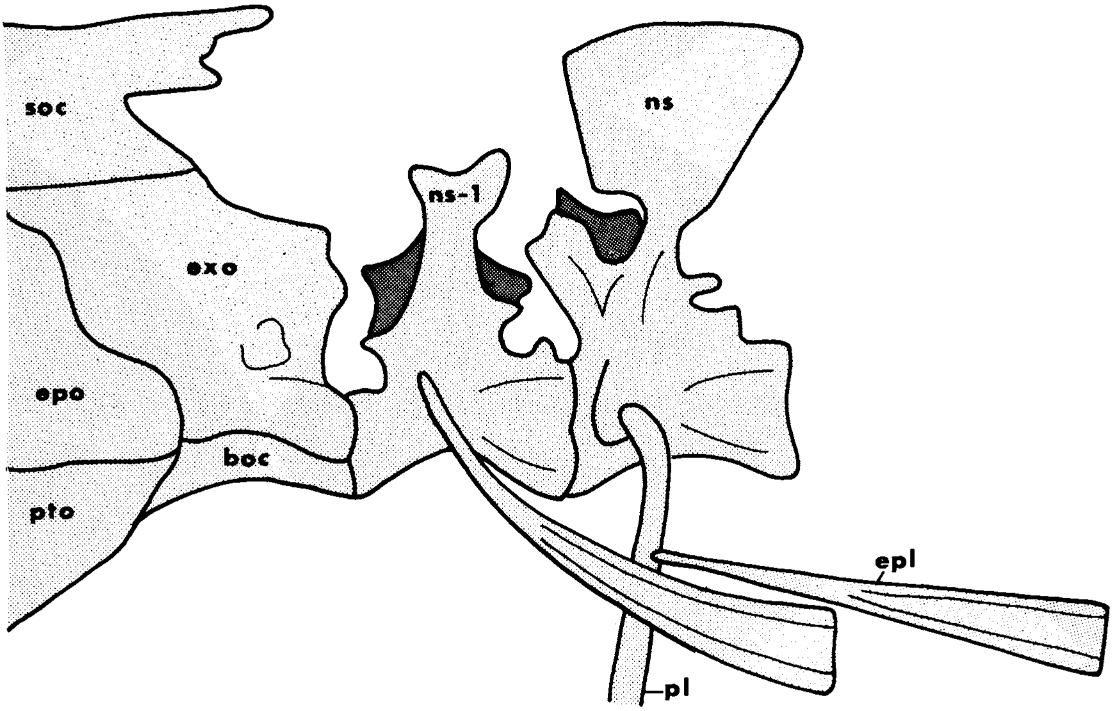

FIG. 26. Diagrammatic representation of the posterior region of the skull and attachment of first vertebra, lateral view, of *Aphyosemion occidentale*. Posttemporal removed.

morph, and paracanthopterygian lineages. Karyotypes of 53 species within the family Cyprinodontidae (including *Oryzias latipes*) and those of 19 species of poeciliid fishes were listed. Within the cyprinodontiforms, as well as all teleosts, the usual haploid chromosome number is 24. In poeciliids the number ranges from 23 to 25; in cyprinodontiforms from nine to 25. Scheel (1968) stated that only among the aplocheiloid fishes within the family Cyprinodontidae did the haploid chromosome number reach 25; therefore, he concluded that this is perhaps the primitive number for aplocheiloids. In light of present findings concerning the nonmonophyletic nature of the cyprinodontids, inclusion of the poeciliids indicates that (1) the haploid number of 25 is attained in cyprinodontiforms other than aplocheiloids, and that (2) it is logical to conclude on the basis of outgroup comparison that n = 24 is basic for aplocheiloids, as well as cyprinodontiforms as a whole.

In species of *Aphyosemion* (which includes the species placed in *Roloffia* in Gyldenholm and Scheel) and *Nothobranchius*, the number ranges from nine to 23 (Scheel, 1968). Among the nominal species of *Epiplatys*, the haploid chromosome number ranges from 17 to 25; it is 24 for the type species of the genus, *E. sexfasciatus*. Among the nominal species of *Aplocheilus*, the haploid number ranges from 18 to 25; it is 18 for the type of the genus, *A. panchax*. *Pachypanchax playfairi* is reported to have 24 haploid chromosomes, as does *Aphyoplatys duboisi*.

Scheel (1968) maintains that the type of chromosome reduction differs in the genera *Epiplatys* and *Aplocheilus* from that in the *Aphyosemion-Nothobranchius* group. That is, in the former genera, the reduction involves the production of large metacentric elements with a subsequent loss of the smaller metacentrics. In the latter genera, the reduction involves the production of large acrocentric elements, accompanied by loss of the smaller elements. White (1968 in Scheel) maintained that such so-called superacrocentrics could arise from pericentric inversions in metacentric elements from the same size. While this could account for the difference in karyological morphology in these two groups of Old World aplocheiloids, Scheel correctly maintains that there are no indications the superacrocentrics were produced in this manner.

In one species of Neotropical aplocheiloids, *Cynolebias* (*Cynopoecilus*) *melanotaenia*, the superacrocentrics occur and the haploid chromosome number of the current aquarium strain is 22 (Scheel, 1968).

The occurrence of superacrocentrics within another group of aplocheiloid fishes indicates that they are not unique to fishes of the *Aphyosemion-Nothobranchius* group, and also that chromosome reduction is not limited to the Old World aplocheiloids. Therefore, the division of Old World aplocheiloids into two groups on the inferred mode of reduction is suspect since the polarity of this reduction cannot be determined. We are left with the character of reduction of chromosomes which is useful in a phylogenetic analysis if it can be correlated with characters from a presumed independent source. Such is the case with the bifid epipleural ribs and slender posterior extension of the vomer used here.

### SUMMARY OF DERIVED CHARACTERS

1. Bifid epipleural ribs.
2. Attenuate posterior process of the vomer.
3. Reduced chromosome number.

### RELATIONSHIPS OF THE *Aphyosemion-Nothobranchius* GROUP

Among those species of *Epiplatys* with low haploid numbers, the following have been examined and possess weakly bifid epipleural ribs: *E. bifasciatus* (n = 20) and *E. spilargyreia* (n = 17). Thus, it appears that on the basis of these two characters certain species of *Epiplatys* may be more closely related to the *Aphyosemion-Nothobranchius* group than to *Epiplatys*, or else the character of bifid epipleural ribs is derived for Old World aplocheiloids. I suggest that no synonymies of Old World genera be undertaken unless the generic limits are formally defined in terms of shared derived characters drawn from a survey of all species for such characters.

*Adamas formosus* (new genus and species described by Huber, 1979) has not been examined. It is placed in this group on the basis of overall external morphology, color pattern and sexual dimorphism as noted from a photograph included in the description. It appears to be most closely related to the primitive species of *Aphyosemion* as described below. Thus, I cannot accept Huber's suggestion that *Adamas* is intermediate between the procatopines and Old World aplocheiloids. Its precise placement within one of the existing supraspecific subdivisions of *Aphyosemion* will require an examination of material.

Annualism: Annualism means that the fertilized egg and embryo exhibit diapause. The species included in the *Aphyosemion-Nothobranchius* group are both annual and nonannual. All members of the *Aplocheilus-Pachypanchax-Epiplatys* group are nonannual. The nonannual members of *Aphyosemion* are *Archiaphyosemion, Mesoaphyosemion, Kathetys, Chromaphyosemion, Diapteron, Aphyosemion,* and *Parepiplatys*. The annual species are in *Raddaella, Paraphyosemion, Paludopanchax, Gularopanchax, Callopanchax, Fundulopanchax,* as well as the subgenera of *Nothobranchius* and in *Fundulosoma*. Members of the genus *Chromaphyosemion* have been referred to as semiannual (e.g., Radda, 1979) because the eggs were observed to tolerate partial drying in the field. However, since all annuals, including so-called true annuals such as *Austrofundulus transilis* can be water-incubated (Wourms, 1972a) it is perhaps more appropriate to refer to the semiannual species as nonannual unless diapause can be demonstrated. Otherwise nothing more than the tolerance of desiccation has been demonstrated.

In addition to being annual, species of the genera *Fundulosoma* and *Nothobranchius* have oval rather than the more typical round eggs of other aplocheiloids (Scheel, 1968).

Swimbladder: The swimbladder of the aplocheiloids typically extends posteriorly beyond several hemal arches, as in the *Aplocheilus-Pachypanchax-Epiplatys* group and *Aphyosemion petersi*. Failure of the swimbladder to extend beyond more than the first pair of hemal arches in *Paludopanchax, Gularopanchax, Callopanchax, Fundulopanchax, Raddaella, Paraphyosemion, Nothobranchius,* and *Fundulosoma* is interpreted as a derived character of the included species.

Dorsal Fin Position and Ray Number: The most primitive position of the dorsal fin for aplocheiloids is inferred to be the general condition for Old and New World genera in which the dorsal fin is set back on the body approximately opposite the last third of the anal fin. Dorsal fin rays typically number seven to 10, though the number can be slightly higher. These primitive conditions occur in the following subgenera of *Aphyosemion*: *Archiaphyosemion, Mesoaphyosemion, Kathetys,* and *Aphyosemion,* as well as *Adamas*. A second group of subgenera have a dorsal fin which is slightly elongate (generally from 10–14 rays) and situated over the first quarter of the anal fin. In this group are the subgenera *Chromaphyosemion* and *Diapteron*.

A third group of *Aphyosemion* subgenera (*Paludopanchax, Gularopanchax, Callopanchax, Fundulopanchax, Raddaella,* and *Paraphyosemion*) and *Fundulosoma* and *Nothobranchius* have an elongate dorsal fin of over 14 dorsal fin rays the origin of which is opposite the anal origin.

Cephalic Sensory Pores and Squamation: One character which does not seem to be useful in separating these subgenera into groups is the open versus closed frontal neuromast pattern. Clausen (1966) first used the closed pattern as a defining character of a new genus *Roloffia* (=*Callopanchax* Myers). In the closed pattern, the two frontal neuromasts are encircled by a rim of epidermis, whereas in the closed pattern the two neuromasts lie separated by a ridge of epidermis. Scheel (1968) published photographs of the two conditions, and used this character to place *Aphyosemion petersi* in the genus *Callopanchax,* along with the more apomorphic *occidentale*. Radda (1977) recognized the apparent unnatural status of *Callopanchax* as thus constituted and placed *petersi* in his *Archiaphyosemion,* where on the basis of the above characters, it more properly belongs.

The closed frontal neuromast pattern was used again by Clausen (1967) to separate the species of his *Parepiplatys* from the rest of the *Epiplatys* species. Scheel (1968) reports that in a brood of *Pachypanchax playfairi,* some individuals developed with the open pattern and some with the closed. Thus, the character seems of doubtful significance for a phylogenetic study, and therefore, fails as a defining character of *Callopanchax*.

The preopercular canal is present in all Old World aplocheiloids and typically opens to the outside by a series of pores (fig. 13A). In the subgenera of *Nothobranchius* and in *Fundulosoma thierryi,* there are no pores, as the canal is open to the outside all along the margin of the preoperculum.

SUBGROUP DEFINITION AND COMPOSITION: I conclude that (1) the genus *Aphyosemion* as currently constituted is not monophyletic; and (2) the annual species previously assigned to *Aphyosemion* are most closely related to the species of *Nothobranchius* and *Fundulosoma*. Annualism is thus postulated to have arisen just once within the Old World aplocheiloids, as may also be true of Neotropical aplocheiloids.

Division of species of the *Aphyosemion-Nothobranchius* group on the basis of dorsal fin position and ray number is problematic. The position of the dorsal fin is variable even among individuals of the same species. However, the species of *Aphyosemion* may be grouped artificially into two categories; those with from seven to 14 dorsal fin rays and the dorsal situated no farther forward than opposite the first quarter of the anal fin; and those with more than 14 dorsal fin rays and the dorsal situated over the anal fin origin or just slightly before or after.

Species groups with a posterior dorsal fin and low dorsal-fin ray number are nonannual and have a swimbladder extending beyond the first hemal arch. They include *Aphyosemion, Archiaphyosemion, Mesoaphyosemion, Chromaphyosemion, Diapteron,* and *Kathetys.* Since they share only primitive characters, these subgenera are not considered to form a monophyletic group. I suggest that they be referred to the genus *Aphyosemion,* however, they will not be formally synonymized with the genus since the monophyletic nature of the group is not implied.

Species groups with an anterior dorsal fin and high fin ray number are annuals that have a swimbladder which does not extend posteriorly beyond the first hemal arch. They include *Raddaella, Paludopanchax, Gularopanchax, Callopanchax, Fundulopanchax, Paraphyosemion, Fundulosoma,* and *Nothobranchius.*

Species of the genera *Fundulosoma* and *Nothobranchius* both share the derived state of the interarcual cartilage as described, oval eggs, and an open preopercular canal. The sole species of *Fundulosoma* may be distinguished from all species included in *Nothobranchius* by the forked posttemporal, and the caudal fin extensions of the males. However, since *Fundulosoma* is monotypic, there is no reason to separate it from the rest of the *Nothobranchius* species. Therefore, I consider it to be a junior synonym of *Nothobranchius.* It may be considered as the most primitive *Nothobranchius* species.

The remaining subgenera of *Aphyosemion* have no generic reference if they are excluded from *Aphyosemion* and hypothesized to be more closely related to the species of *Nothobranchius* as defined above. Among the names of subgenera within this group, *Fundulopanchax* Myers is the oldest and therefore the name which will be used to reference the annual *Aphyosemion* species. However, it is not implied that this group itself is monophyletic since some members may be more closely related to *Nothobranchius* than to each other. Therefore, no synonymy of the subgenera is suggested at this time.

### THE *Aplocheilus-Pachypanchax-Epiplatys* GROUP

Species in this group are currently classified in three genera (*Aplocheilus, Pachypanchax* and *Epiplatys*). *Epiplatys,* in turn, is divided into four subgenera (*Lycocyprinus, Parepiplatys, Aphyoplatys,* and *Pseudepiplatys*).

CHARACTER ANALYSIS: Jaw: Typically, the head is greatly flattened, as is the upper jaw, resulting in a dorsal profile which has been referred to as pikelike. (When first described, *Aplocheilus panchax* was placed in the genus *Esox.*) The flattened upper jaw is represented internally by broadly expanded premaxillary ascending processes (fig. 4A). In addition to this upper jaw characteristic there is a concordant feature of the lower jaw which contributes to the flattened appearance of the mouth. As illustrated for *Aplocheilus panchax* (fig. 27) there is a unique, large coronoid process on the dentary which overlaps the dorsal extension of the articular. There is no such process in the *Aphyosemion-Nothobranchius* group (e.g., fig. 31C).

Caudal fin: The internal supports of the caudal fin differ among adults of the three genera although they are similar in juveniles. In *Aplocheilus,* the upper hypural plate is divided in two (fig. 2D). In *Epiplatys,* the upper and lower hypural plates are separate and never fused together to form an hypural fan. In at least one species, *E. sexfasciatus,* there is evidence of a line of division in the upper hypural plate, suggesting the division seen in species of *Aplocheilus.*

In adult *Pachypanchax,* the hypural plates are fused to form an hypural fan, as is the case in *Nothobranchius, Fundulosoma,* and some species of *Aphyosemion,* a group of Neotropical aplocheiloids, and most, but not all, the cyprinodontoids. However, in juvenile lab-reared *Pachypanchax playfairi* the dorsal and ventral hypural plates have an evident joint, and there is also such a suture between the dorsal and ventral portions of the upper hypural plate. In *Fundulus majal-*

*is,* a funduline, and in *Nothobranchius guentheri,* species in which adults have a hypural fan, the juveniles possess a hypural fan, even at the stage of a cartilaginous precursor of the hypural elements. Therefore, given that the aplocheiloids form a monophyletic group, the separate hypurals of the *Aplocheilus-Pachypanchax-Epiplatys* group are an indication of a secondarily derived condition.

Dorsal Gill Arches: The *Aplocheilus-Pachypanchax-Epiplatys* group exhibits a derived feature of the dorsal gill arches. Typically among cyprinodontiforms, an uncinate process from the third epibranchial articulates via a cartilage with a corresponding process on the fourth epibranchial. The uncinate process of the fourth epibranchial, however, is absent in these three genera. The fourth epibranchial is present as a slender element (fig. 24A) which has no point of articulation to the third.

### SUMMARY OF DERIVED CHARACTERS

1. Broadly expanded premaxillary ascending processes.
2. Coronoid process on dentary overlaps dorsal extension of articular.
3. Separate upper hypurals at least in juveniles.
4. Loss of the uncinate process on the fourth epibranchial.

*Aplocheilus-Pachypanchax-Epiplatys* GROUP RELATIONSHIPS: On the basis of the following characters, I conclude that *Pachypanchax* and *Aplocheilus* are more closely related to each other than either is to *Epiplatys*; therefore, placing *Epiplatys* in synonymy with *Aplocheilus* (Scheel, 1972; Radda, 1973) and excluding *Pachypanchax* would create a paraphyletic genus.

Posttemporal: The posttemporal is typically a forked bone attaching distally to the supracleithrum and proximally to the epiotic dorsally and the exoccipital ventrally. In Old World aplocheiloids, the supracleithrum is not a distinct element, thus the posterior extension of the posttemporal-supracleithrum attaches directly to the cleithrum. Among several groups of cyprinodontiforms, the lower limb of the posttemporal extending to the exoccipital is unossified, and represented only by a ligament. Within the aplocheiloids, this occurs in the genera *Aplocheilus* and *Pachypanchax* and in *Nothobranchius.* It is fully forked in all species of *Epiplatys* and *Aphyosemion* examined, as well as in *Fundulosoma thierryi.* The lower limb being represented by an unossified ligament is most parsimoniously assessed as independently derived in *Aplocheilus* and *Pachypanchax* and *Nothobranchius.*

Hypobranchial Teeth: Both *Aplocheilus* and *Pachypanchax* have patches of teeth on the second and third pair of hypobranchials, as well as on the fourth ceratobranchials. Such teeth are typically found on the fourth ceratobranchials of atherinomorphs except when lost or reduced as in a group of the Neotropical aplocheiloids. Teeth on the hypobranchial elements, however, have not been found except in these two genera of aplocheiloids and in two cyprinodontoid genera *Anableps* and *Oxyzygonectes.* Thus, the presence of hypobranchial teeth is considered to be independently derived in these two cases.

Dorsal Ocellus: A dorsal ocellus is present in all females of *Aplocheilus* and *Pachypanchax playfairi.* The ocellus is developed also in males of several species of *Aplocheilus* such as in *A. panchax.* The dorsal ocellus is absent in all other Old World aplocheiloids. The genus *Pachypanchax* contains two species, *playfairi* and *homalanotus.* The dorsal ocellus is reported to be absent from both males and females of the latter species (Scheel, 1968). Only one specimen of *homalanotus* was examined, and the species' continued placement in *Pachypanchax* should perhaps be investigated.

Orbital Rim: As discussed for the defining characters of the aplocheiloids, *Aplocheilus* and *Pachypanchax* have an orbital rim which is attached ventrally and folded under the frontals dorsally. This is in contrast to the condition in all other aplocheiloids in which the orbital rim is attached all along its perimeter.

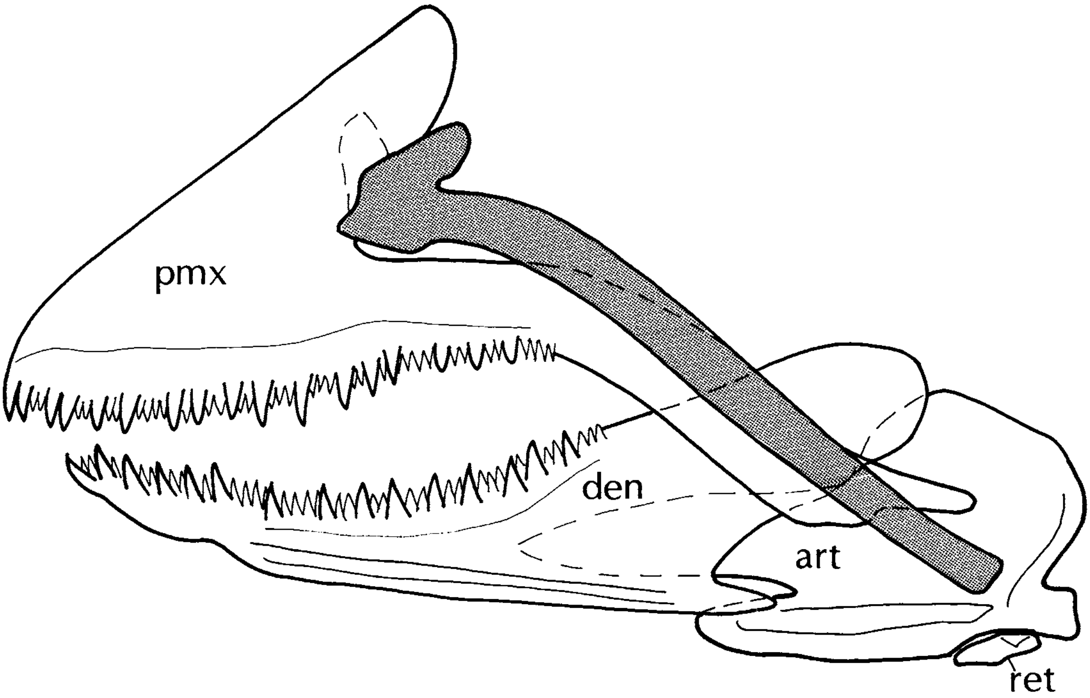

FIG. 27. Diagrammatic representation of upper and lower jaw of *Aplocheilus panchax*, lateral view. Maxilla is stippled.

Caudal Fin Margin: In *Pachypanchax playfairi* and a number of species of *Aplocheilus,* including *panchax,* there is a dark line of pigment on the caudal fin. Such a margin is not found elsewhere within the aplocheiloids, and as such it is considered uniquely derived.

SUBGROUP DEFINITION AND COMPOSITION: *Pachypanchax* may be distinguished from the species of *Aplocheilus* and *Epiplatys* by lateral scales in males which are angled away from the body, and by the fusion of the hypural plates in adults into an hypural fan. The former character refers to a long-known feature of *playfairi.* The scales stand away from the body in live adult males and give the impression that the individual is suffering from dropsy.

*Aplocheilus* may be distinguished from the species of *Pachypanchax* and *Epiplatys* by an attenuate lower jaw and medially greatly expanded premaxillary ascending processes.

The species of *Epiplatys* considered to be part of this monophyletic group may be distinguished only by its lack of the derived characters present in *Pachypanchax* and *Aplocheilus*. *Epiplatys* has a forked posttemporal, a completely attached orbital rim, and lacks a dorsal ocellus, darkened caudal fin margin and teeth on the second and third hypobranchials. *Epiplatys,* therefore is not definable as a monophyletic group; it may eventually be restricted to the type species, *sexfasciatus* Gill, and closely allied species.

CLADISTIC SUMMARY OF OLD WORLD APLOCHEILOIDS: Old World aplocheiloids are divisible into two groups. The *Aplocheilus-Pachypanchax-Epiplatys* group is distinguished from the other Old World aplocheiloids by the following derived characters: a broad, flattened, upper jaw effected by expanded premaxillary ascending processes and an expanded coronoid process on the dentary, a bifurcate upper hypural plate in juveniles and some adults; and the loss of the uncinate process on the fourth epibranchial.

*Aplocheilus* and *Pachypanchax* are assessed as sister genera on the basis of the following derived characters: teeth on the second and third hypobranchials; lower limb of the posttemporal represented by an unossified ligament; a dorsal ocellus in females; an orbital rim attached only ventrally; and a dark caudal fin margin.

*Pachypanchax* is defined by two derived characters: fusion of the upper and lower hypural plates into a hypural fan in adults; and, lateral scales of males angled away from the body.

*Aplocheilus* is defined by an attenuate lower jaw and premaxillary ascending processes expanded medially and overlapping.

The genus *Epiplatys* as recognized here cannot be defined as a monophyletic group. Some species currently referred to the group may prove to be more closely related to forms of *Aphyosemion* and *Nothobranchius*.

The *Aphyosemion-Nothobranchius* group is defined by the following derived characters: bifid epipleural ribs; attenuate posterior expansion of the vomer; and a reduced chromosome number.

The subgenera of *Aphyosemion* may be grouped into the following two categories:

The *Aphyosemion* group comprising the subgenera *Aphyosemion, Archiaphyosemion, Mesoaphyosemion, Kathetys, Diapteron,* and *Chromaphyosemion,* and the genus *Adamas*. They are all nonannual, possess a dorsal fin of from seven to 14 rays which is situated no farther anterior than opposite the first quarter of the anal fin origin, and have a swimbladder which extends posteriorly to the first one or two hemal spines.

The *Fundulopanchax* group comprising the subgenera *Fundulopanchax, Gularopanchax, Raddaella, Callopanchax, Paraphyosemion,* and *Paludopanchax* which shares with the species of *Nothobranchius* and *Fundulosoma* the following derived characters: dorsal fin rays increased to 14 or more; dorsal situated opposite the anal fin origin or just slightly in front or behind the origin; and swimbladder not expanded past the first hemal arch. All included species are annual. Monophyly of *Aphyosemion* and *Fundulopanchax* is not implied.

*Fundulosoma* and *Nothobranchius* share the following derived characters: preopercular canal open, not represented by pores; a derived position of the interarcual cartilage and oval eggs. The species of *Nothobranchius* and its included subgenera may be separated from *Fundulosoma thierryi* on the basis of the following derived characters: lower limb of posttemporal represented only by an unossified ligament and all fins rounded with no caudal fin extensions. However, *thierryi* is considered to be the primitive member of the genus *Nothobranchius* since the recognition of a monotypic genus at this position in the phylogenetic analysis is uninformative with respect to the interrelationships of included species.

## CYPRINODONTOIDS (GROUP C)

The cyprinodontoids as the term is used in this study refers to the fishes of the four viviparous families, the Poeciliidae, Goodeidae, Jenynsiidae and Anablepidae, and the cyprinodontid subfamilies Fundulinae, Lamprichthyinae, Fluviphylacinae, Cyprinodontinae, Aplocheilichthyinae, Orestiatinae and Pantanodontinae (see table 2). The subgroups are referred to using the vernacular names as defined previously. Prior to this study, these fishes have not been considered together as a group without including the aplocheiloids. However, together they form one of the most well-corroborated monophyletic groups of fishes.

Together these groups comprise nearly 400 species, slightly less than its sister group, the aplocheiloids. Their diversity includes oviparity, ovoviviparity to viviparity; unicuspid, bicuspid, tricuspid, or no teeth in the jaws; and a size range from the diminutive male *Heterandria formosa* of the poeciliid fishes which matures at a standard length of approximately 8 mm. (Rosen and Bailey, 1963) to the large females of the viviparous *Anableps* which reach a standard length of over 300 mm. (Miller, 1979). They are found in fresh, brackish and salt water, and are distributed pantropically as well as in temperate Laurasia from North America and as far east as Iran.

CHARACTER ANALYSIS: Gill Arches: Several derived characteristics of the gill arches distinguish the cyprinodontoids from the aplocheiloids and all other atherinomorph fishes. The first of these is the presence of just two basibranchials in the ventral gill arch skeleton. In aplocheiloids, as in all other atherinomorphs, as well as most other acanthopterygian fishes, there are three ossified basibranchials. These lie medially in a straight line behind the basihyal and extend posteriorly to the angle created by the fifth ceratobranchials (fig. 11). The basihyal and basibranchials are initially represented in ontogeny by a continuous rod of cartilage known as the copula. This precursor is replaced in ontogeny by separate basihyal and basibranchial ossifications. In the aplocheiloids, as illustrated for *Nothobranchius melanospilus* (fig. 11A), the basihyal is followed posteriorly by three ossified basibranchials. In contrast, within all cyprinodontoids, the first ossified basibranchial is absent, whereas the second and third are present in much the same position as those of the aplocheiloids (fig. 11B).

Two ossified basibranchials occur elsewhere in the acanthopterygian fishes, notably in synbranchid eels. Rosen and Greenwood (1976) report that the condition of two ossified basibranchials is effected by the fusion of the first basibranchial with the basihyal. In the cyprinodontoids, however, there is no such apparent fusion of the first basibranchial to either the basihyal or the second basibranchial. In addition, the section of the cartilaginous precursor of the first basibranchial is absent in adult cyprinodontoids; thus, the condition of the two ossified basibranchials may be described as the loss of the first basibranchial.

Typically among atherinomorphs, as for most teleosts, the hyoid bar is composed anteriorly of two hypohyals. The two elements, a dorsal and a ventral hypohyal, articulate with the anterior process of the anterior ceratohyal. Typically among aplocheiloids, and most other cyprinodontiforms, there is an extension of the anterior ceratohyal under the ventral hypohyal. This is the case as illustrated for *Pachypanchax playfairi* (fig. 28A).

In all cyprinodontoids, the dorsal hypohyal is absent. The anterior ceratohyal typically retains its anterior extension under the ventral hypohyal, as in *Oxyzygonectes dowi* (fig. 28B). However, in the poeciliid fishes, *Fluviphylax* and procatopines there is no distinct anterior extension of the anterior ceratohyal, and the remaining ventral hypohyal is present as a cap of bone over the end of the anterior ceratohyal as in *Procatopus gracilis* (fig. 28C). In *Pantanodon madagascariensis,* there is no extension of the anterior ceratohyal under the ventral hypohyal; however, there appear to be two ossification centers in the cap of cartilage present on its anterior face. These would probably be interpreted as a dorsal and a ventral hypohyal; however, in the light of the other evidence which clearly places *Pantanodon* as a member of the cyprinodontoids with a derived state of the anterior ceratohyal, I interpret the cartilaginous cap with its two ossification centers as a secondarily derived condition which is most like that described for the poeciliids, procatopines and *Fluviphylax*.

In the aplocheiloids, the typical state of the interarcual cartilage is as an elongate rod approximately equal in length to the epibranchials. It is absent among aplocheiloids in the genus *Pterolebias* and was found reduced in *Rachovia maculipinnis*. In all cyprinodontoids, the interarcual cartilage is reduced to approximately one half the length of the epibranchials (fig. 6B). (The reduced condition in *maculipinnis* is considered secondarily derived within the aplocheiloids.)

Jaw and Jaw Suspensorium: In cyprinodontiforms as a whole, as is true for many other, but not all atherinomorphs, there are no dermal jaw suspensorium elements. Sim-

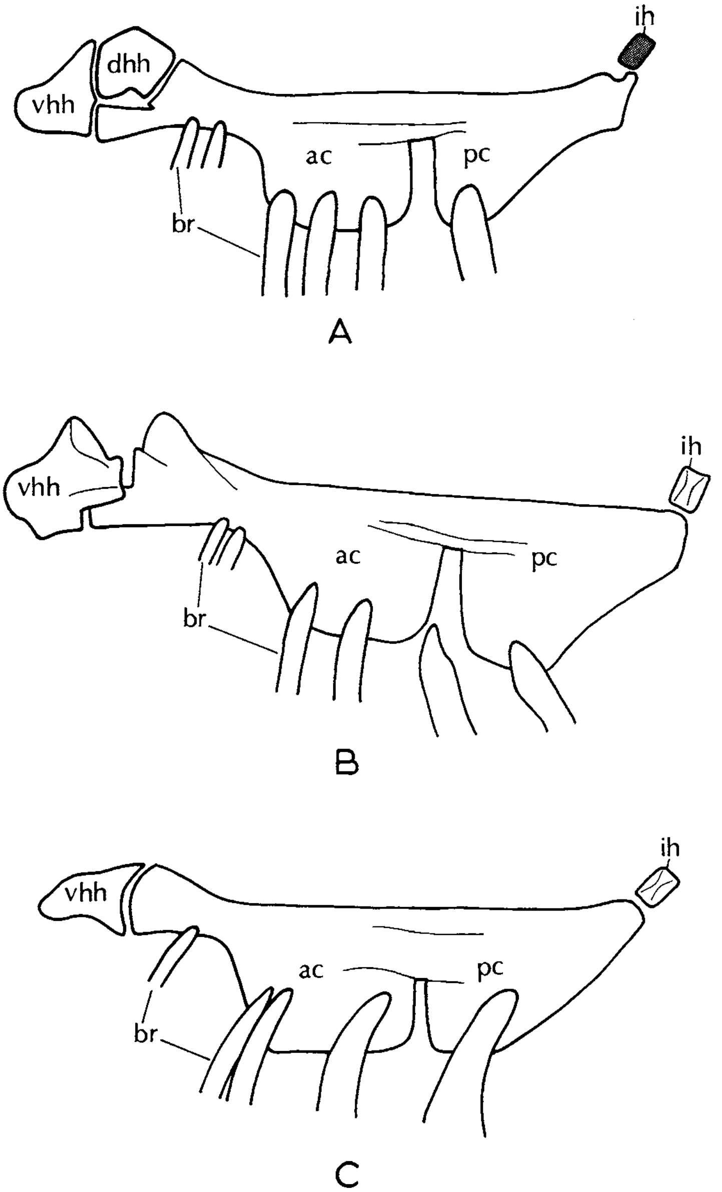

FIG. 28. Diagrammatic representation of hyoid bar of A. *Rivulus harti*; B. *Oxyzygonectes dowi*; C. *Procatopus gracilis*. Cartilage is stippled.

ilarly, the ectopterygoid is also lacking in many atherinomorphs including cyprinodontiforms, although the identification of this state has not been made consistently in atherinomorph studies. Rosen (1964) illustrated a section of the jaw suspensorium of *Xiphophorus helleri*, a poeciliid, and identified the ventral extension of the autopalatine as the ectopterygoid, although it is not present as a distinct bone, and no joint lines are visible between it and the autopalatine.

In some exocoetoids in which the ectopterygoid is a separate bone (e.g., in *Parexocoetus brachypterus*) there is also a ven-

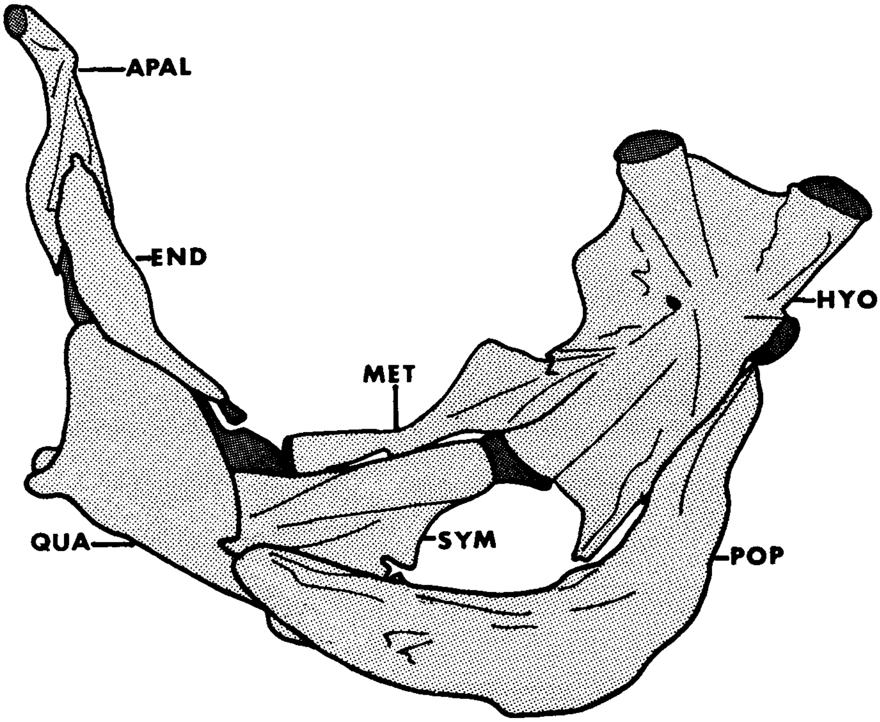

FIG. 29. Diagrammatic representation of jaw suspensorium of *Cynolebias whitei*.

tral extension of the autopalatine. Thus the ectopterygoid is considered to be lost in certain atherinomorphs including the cyprinodontiforms. The degree of the extension on the autopalatine varies among cyprinodontiforms. In the aplocheiloids, as in most other atherinomorphs, the autopalatine extension is short and does not reach the quadrate. In contrast, in the cyprinodontoids, as illustrated for *Procatopus gracilis* (fig. 30), the extension of the autopalatine is enlarged and covers part of the quadrate.

In addition to having an enlarged ventral process, the head of the autopalatine is set at an angle to its arm. In the aplocheiloids (fig. 29), as is true generally for atherinomorphs, the head of the autopalatine is straight, whereas in the cyprinodontoids (fig. 30) the head of the autopalatine is distinctly offset. There is also a bony flange which extends posteriorly giving the anterior extension of the autopalatine the shape of a hammerhead. In a group of the cyprinodontoids, which include goodeids, *Empetrichthys*, and *Crenichthys*, the head of the autopalatine is reduced to a nubbin, a condition considered to be secondarily derived. It is readily distinguished from the aplocheiloid condition in that the head is blunt, rather than slender.

A third derived character of the jaw suspensorium of the cyprinodontoids is the loss of the metapterygoid (see figs. 29 and 30). The metapterygoid is also absent in the adrianichthyoids *Oryzias* and *Horaichthys*; but, since they possess none of the derived characters for cyprinodontiforms, their loss of the metapterygoid is inferred to be independent.

The cyprinodontiforms exhibit a derived state of the premaxilla characterized by the two-part alveolar process. The superficial division of the adductor mandibulae inserts via a tendon to the middle of the arm of the

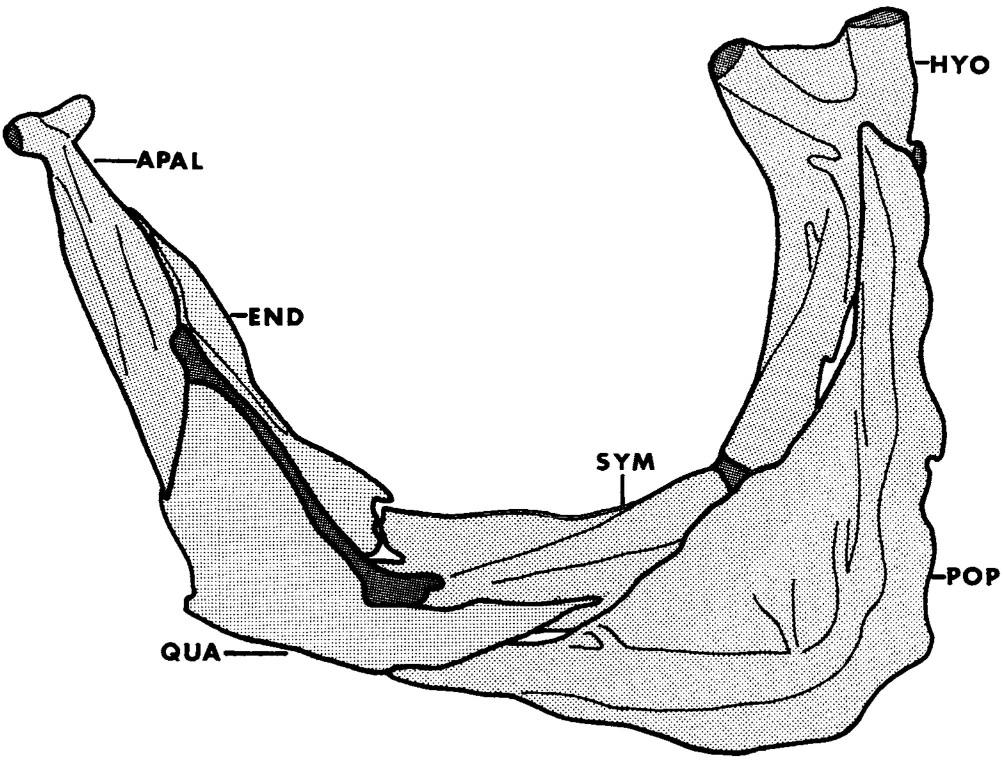

FIG. 30. Diagrammatic representation of jaw suspensorium of *Procatopus gracilis*.

maxilla, whereas the more anterior layers insert on the posterior extension of the alveolar arm.

In the cyprinodontoids, the alveolar arm is distinctly S-shaped (fig. 3B), as a result of bending and enlarging of the post-maxillary process. This is the condition typical of cyprinodontoids, and although the arm undergoes modifications in several of its subgroups, it can always be distinguished from that of the aplocheiloids by the posterior indentation.

In the aplocheiloids, the dentary is a relatively thin bone, which carries a distinct sensory canal (fig. 31C). In *Menidia* (fig. 31B), as in many other atherinoids, there is a large coronoid process on the dentary; yet, ventrally, the bone is unexpanded as in the aplocheiloids. Similarly, in *Oryzias* (fig. 31A) the dentary is unexpanded. In all cyprinodontoids, the dentary is a robust bone (fig. 33) expanded medially, and therefore, carrying the sensory canal along its midline.

There are no ethmomaxillary ligaments present in cyprinodontoids as there are in aplocheiloids. Similarly, there are no ligaments extending from the interior arms of the maxillaries to the middle of the rostral cartilage. In addition, there is no meniscus between the premaxilla and the maxilla. These elements are present, however, in the aplocheiloids and atherinoids (Alexander, 1967b). Hence, their absence in cyprinodontoids is considered derived.

Vomer: The vomer bears teeth in all aplocheiloid species. The state of this character is variable, however. When present, the teeth are usually in a round patch at the anteromedial extension of the vomer, as in *Rivulus* (fig. 17C). In *Aplocheilus* (fig. 17B), the teeth extend across the anterior edge of the vomer. In cyprinodontoids and in ather-

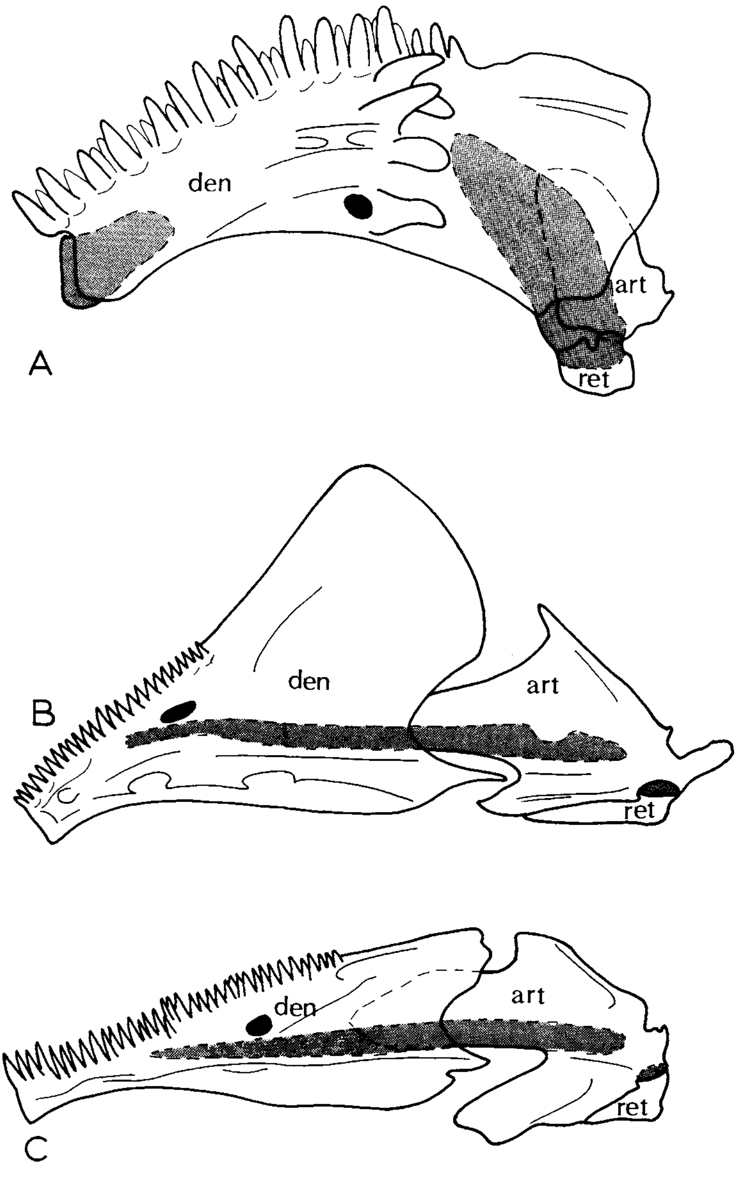

FIG. 31. Diagrammatic representation of lower jaw, lateral view: A. *Oryzias javanicus*; B. *Menidia menidia*; C. *Aphyosemion occidentale*. Cartilage is stippled, Meckel's cartilage is the elongate central element.

inoids the vomer does not possess a medial extension and there are never any teeth on the vomer. Vomerine teeth might, therefore, be derived for aplocheiloids and lost independently in some aplocheiloids and in cyprinodontoids. The usefulness of this character, however, is dubious because its distribution coincides with no other known character.

Loss of First Dorsal Fin Ray: Another derived character which defines the cyprinodontoids as a monophyletic group pertains to

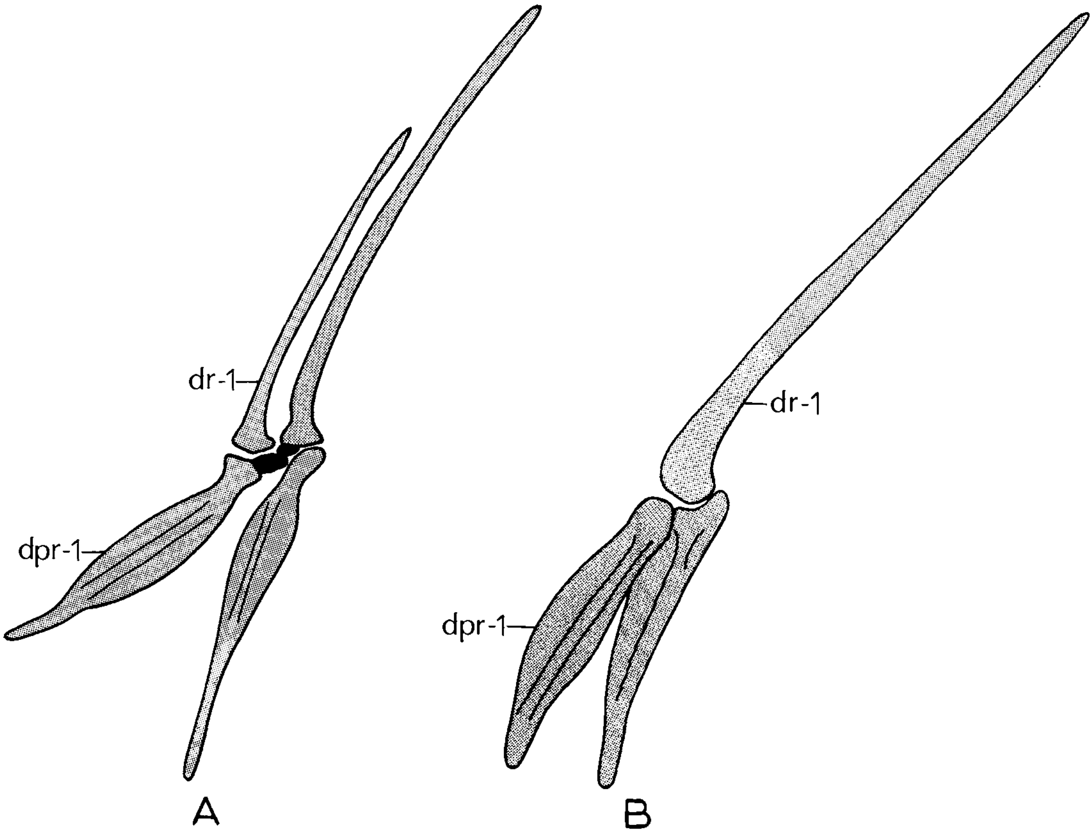

FIG. 32. Diagrammatic representation of first two proximal dorsal radials articulating with two dorsal fin rays in A. *Pachypanchax playfairi*; with one dorsal fin ray in B. *Adinia xenica*.

the number of dorsal fin rays. In all aplocheiloids, there is one dorsal fin ray articulating with each of the first two dorsal radials (fig. 32A). The first dorsal ray is often rudimentary; nonetheless, it is present. In all cyprinodontoids (fig. 32B) the first dorsal ray is apparently lost, and the second remaining ray articulates with the first two proximal dorsal radials.

### SUMMARY OF DERIVED CHARACTERS

1. Two basibranchials in the ventral gill arch skeleton.
2. Loss of the dorsal hypohyal.
3. Reduction of interarcual cartilage to one half its length, relative to that of the aplocheiloids, and the associated placement of the first epibranchial closer to the second pharyngobranchial.
4. Autopalatine with its anterior extension bent sharply and hammer-shaped.
5. Extension of the autopalatine ventrally forming an anterior covering of the quadrate.
6. Metapterygoid absent.
7. Alveolar arm of premaxilla S-shaped.
8. Dentary expanded medially and robust.
9. Loss of an ethmomaxillary ligament.
10. Loss of a ligament from the interior arms of the maxillaries to the middle of the rostral cartilage.
11. Loss of a meniscus from between the premaxilla and the maxilla.
12. Loss of an anterior dorsal fin ray result-

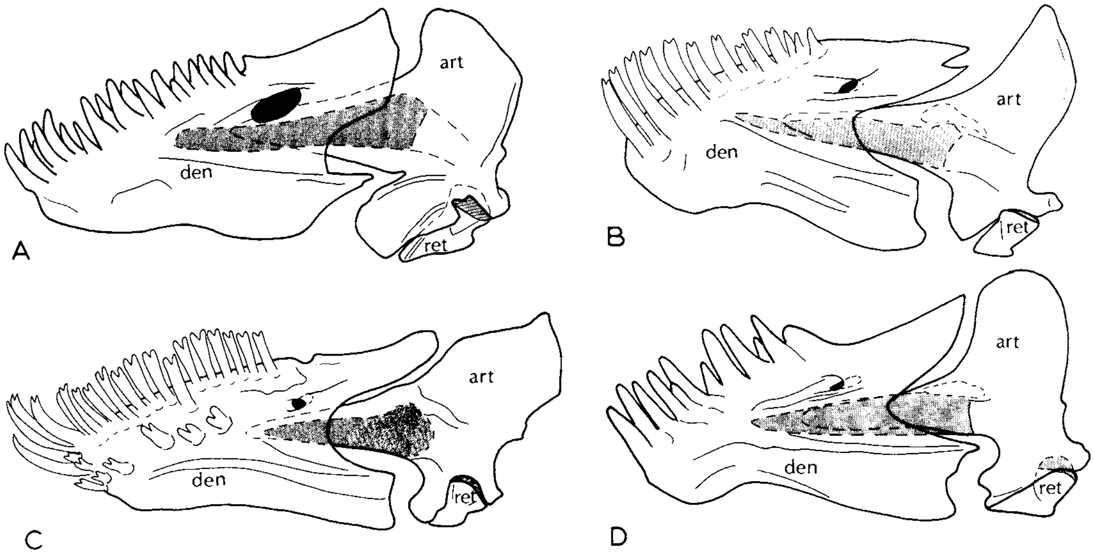

FIG. 33. Diagrammatic representation of lower jaw, lateral view, A. *Profundulus punctatus*; B. *Characodon lateralis*; C. *Crenichthys baileyi*; D. *Empetrichthys latos pahrump*.

ing in the articulation of the first dorsal fin ray with first two proximal radials.

RELATIONSHIPS OF THE CYPRINODONTOIDS: Jaw and jaw suspensorium: The most primitive type of jaw structure within cyprinodontoids is that found in the Central American genus *Profundulus*. The alveolar arm of the premaxilla is indented posteriorly, forming an S-shaped distal process. The dentary (fig. 33A) is expanded medially forming a robust lower jaw. There are no large processes on the dentary or the articular, and the retroarticular is of moderate size.

Premaxillary ascending processes in *Profundulus* are flat and broad (fig. 5B). At their tips sits the large, rectangular rostral cartilage. The interior arms of the twisted maxillaries abut the rostral cartilage and are bound to it by collagen fibers. No ligament from the interior arms to the cartilage has been found, as present in the aplocheiloids and atherinoids, as reported by Alexander (1967b). Similarly, there is no ethmomaxillary ligament, nor is there a meniscus between the premaxilla and maxilla. In other cyprinodontoids, the rostral cartilage is reduced relative to the condition found in *Profundulus*. Alexander (1967b) stated that in *Fundulus* the rostral cartilage is Y-shaped and therefore comes in contact with the hooks on the interior arms of the maxillaries. With the benefit of the counterstaining technique employed throughout this study, it has been determined that the rostral cartilage is not Y-shaped but is represented by, at most, four small discs of cartilage in the fundulines; one is situated posterior, and two smaller elements anterior, to a larger medial cartilage located between the internal hooks of the maxillaries (fig. 5C). These bits of cartilage are held together and to the maxillary by connective tissue fibers, forming what is presumably the "Y-shaped" rostral cartilage of Alexander. Thus, in fundulines as well as in all other cyprinodontoids (excluding *Profundulus*) there has been a loss of contact between the inner arms of the maxillaries and the rostral cartilage, a condition associated with reduction of the cartilage.

In both the fundulines and the Mediterranean genus *Valencia* which has heretofore been classified in the same subfamily as the

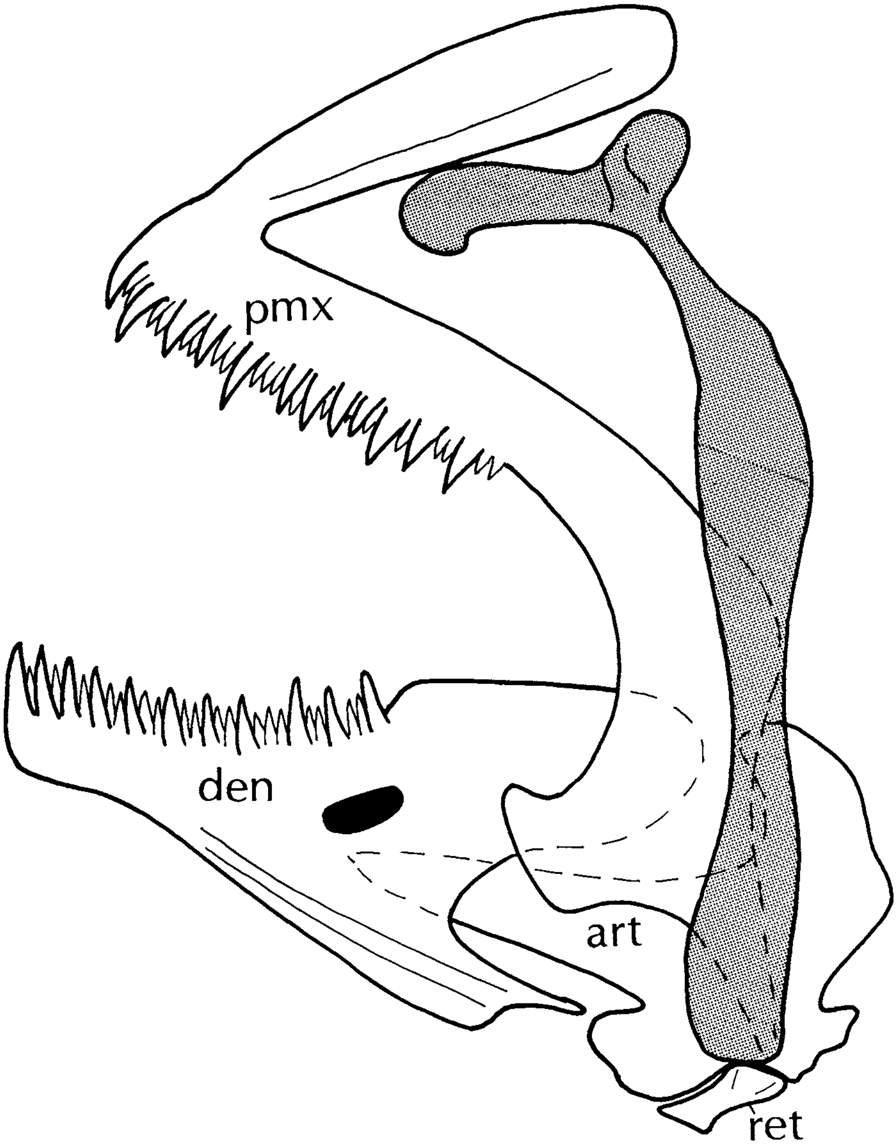

FIG. 34. Diagrammatic representation of upper and lower jaw, lateral view, of *Fundulus diaphanus*. Maxilla is stippled.

fundulines, the premaxillary ascending processes are narrow and elongate (fig. 5D). Narrow premaxillary processes are characteristic of the group of cyprinodontoids excluding *Profundulus*. The elongate processes of fundulines and *Valencia* are considered as stages in a transition series from the broad processes typical of *Profundulus* and the aplocheiloids to the short and narrow processes of the large subgroup of cyprinodontoids comprising the following: *Jenynsia, Anableps, Oxyzygonectes,* the poeciliids, procatopines, *Pantanodon, Fluviphylax,* the goodeids, *Empetrichthys, Crenichthys, Orestias,* the cyprinodontines, *Cubanichthys* and *Chriopeoides*. This large group, plus

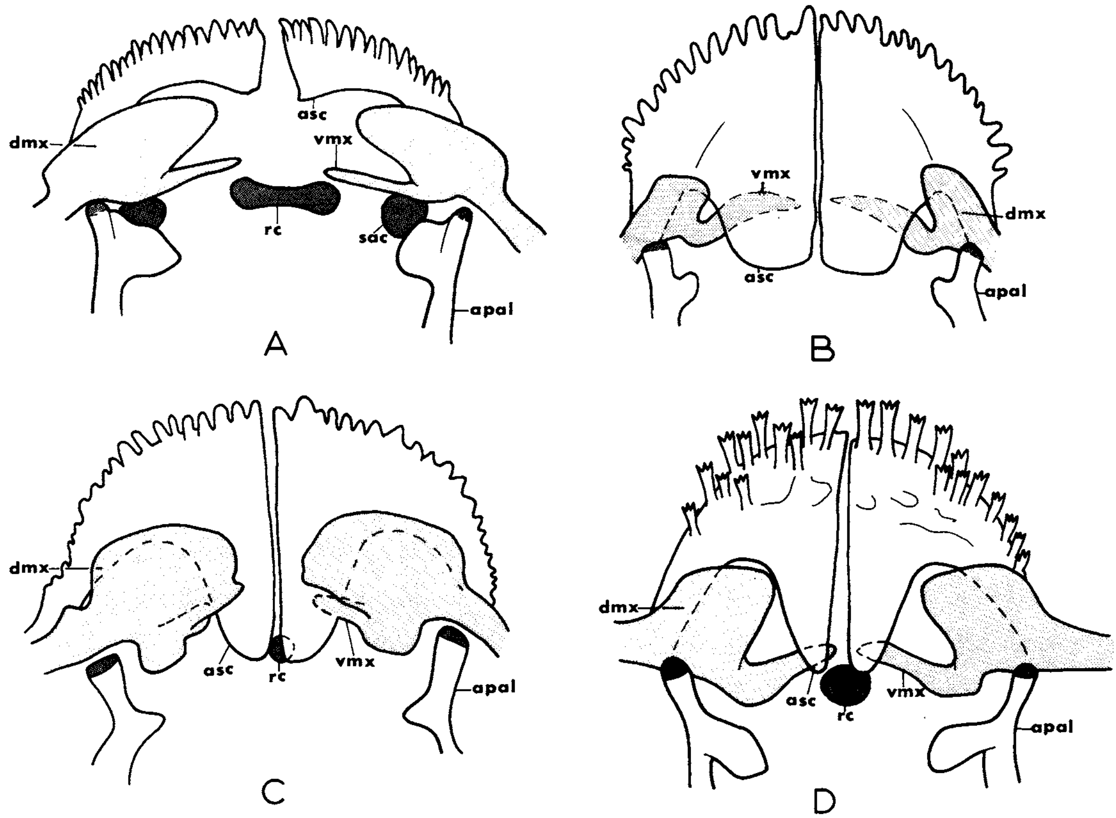

FIG. 35. Diagrammatic representation of the upper jaw in A. *Anableps dowi*; B. *Oxyzygonectes dowi*; C. *Aplocheilichthys johnstoni*; D. *Jenynsia lineata*.

*Valencia*, has attenuate interior arms of the maxillaries, rather than the broad tips associated with *Profundulus* and the aplocheiloids. In addition, they have a maxilla which is straight rather than characteristically twisted as in fundulines, aplocheiloids, and *Profundulus*. The arm does not have a pronounced bend anterior to the autopalatine (as in *Fundulus diaphanus*, fig. 5C), but, it is rather straight and often has a pronounced flat dorsal process which extends anteriorly over the premaxillary ascending processes (fig. 5D).

The fundulines are unique among cyprinodontiforms in having pronounced hooks on the interior arms of the maxillaries (figs. 5C, 34). In addition, the interior arms are directed anteriorly, rather than medially as in other cyprinodontoids. These characters may be considered derived for the fundulines, and therefore define them as a monophyletic group.

*Valencia* shares the derived characters of the rest of the cyprinodontoids as described above; that is, a straight maxilla with attenuate interior arms, and the development of a dorsal extension over the premaxillary ascending processes. *Valencia* is unique among cyprinodontiforms in having very long attenuate dorsal processes of the maxillaries (fig. 5D). In other cyprinodontoids of the large group delimited above, the dorsal processes are rounded when present. Since there are no such dorsal processes in the fundulines, *Profundulus* or aplocheiloids, the polarity of the character is ambiguous. The elongate dorsal processes of *Valencia* may represent the primitive state of the processes

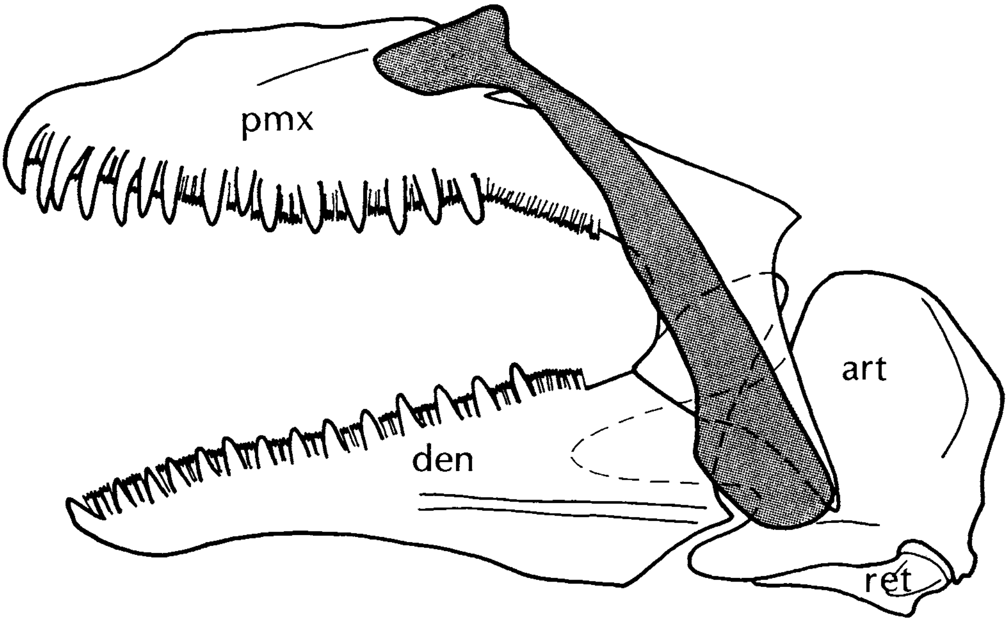

FIG. 36. Diagrammatic representation of upper and lower jaw, lateral view, of *Oxyzygonectes dowi*. Maxilla is stippled.

which are further reduced in the large subgroup; or, the reverse may be true. The polarity of this character may be resolvable with an ontogenetic series of *Valencia*.

The large subgroup minus *Valencia* is defined by having narrow and shortened premaxillary ascending processes, and the rostral cartilage reduced or absent. The dorsal processes of the maxilla are rounded when present. This subgroup may itself be subdivided into two monophyletic groups.

The poeciliids, procatopines, *Fluviphylax, Pantanodon,* and *Oxyzygonectes, Jenynsia* and *Anableps* form a monophyletic group based on three derived jaw characters: the dorsal processes of the maxillaries are indented laterally to form nearly fan-shaped processes; the distal arm of the maxilla is expanded; and the retroarticular is enlarged.

The dorsal process of the maxilla, as in the procatopine *Aplocheilichthys johnstoni* (fig. 35C) and for *Jenynsia lineata* (fig. 35D), has a distinct lateral indentation. The result is a distinct fan-shaped process which projects over the triangular premaxillary ascending processes. The dorsal process is found in this state, as well, in *Anableps* (fig. 35A), *Oxyzygonectes* (fig. 35B), the remaining procatopine genera, and the majority of the poeciliids (e.g., as illustrated in Rosen and Bailey, 1963). In both *Pantanodon* and *Fluviphylax* the dorsal processes are weakly formed; yet, on the basis of characters to be discussed they are considered to be part of this monophyletic group, and their weakly formed processes are considered to be secondarily derived.

The distal arm of the maxilla is enlarged at its most ventral extension (e.g., as in *Oxyzygonectes dowi,* fig. 36) in all members of the group excluding the procatopine genera *Procatopus* and *Hypsopanchax,* and a group of species of *Aplocheilichthys* (e.g., as in *Procatopus gracilis,* fig. 37), in which the distal arm of the maxilla is shortened relative to its condition in the other members of this group.

Similarly, the retroarticular is extremely elongate in *Anableps, Jenynsia* (fig. 38B), *Oxyzygonectes* (fig. 36), and the procatopine

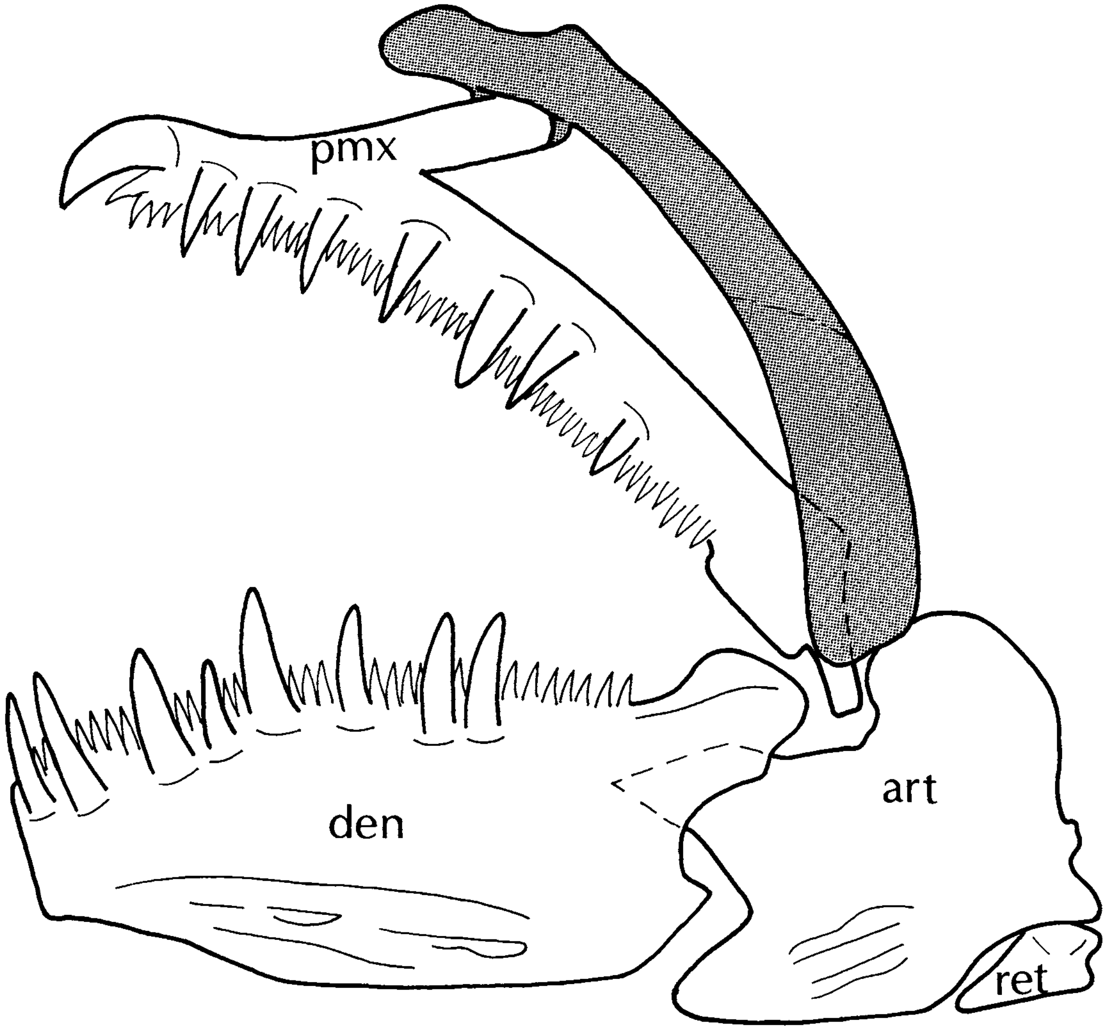

FIG. 37. Diagrammatic representation of upper and lower jaw, lateral view, of *Procatopus gracilis*. Maxilla is stippled.

genera *Aplocheilichthys* (fig. 38C) and *Lamprichthys,* and moderately elongate in *Tomeurus,* the presumed primitive poeciliid. Within *Pantanodon, Fluviphylax,* and *Procatopus* (fig. 37) and *Hypsopanchax,* the retroarticular is reduced.

Thus, the premaxillary and retroarticular characters appear to be correlated. The elongate retroarticular and expanded arm of the premaxilla are a general characteristic of the group, but both of these elements are secondarily reduced in *Hypsopanchax, Procatopus, Pantanodon,* and *Fluviphylax.*

Within this large group, the poeciliids, *Fluviphylax, Pantanodon* and the procatopines are distinguished by the formation of a greatly enlarged dentary. The less expanded dentary of *Jenynsia* (fig. 38B), *Oxyzygonectes* (fig. 36) and *Anableps* is the condition primitive for all cyprinodontoids.

In the poeciliids, procatopines, *Pantanodon* and *Fluviphylax,* the dentary is much

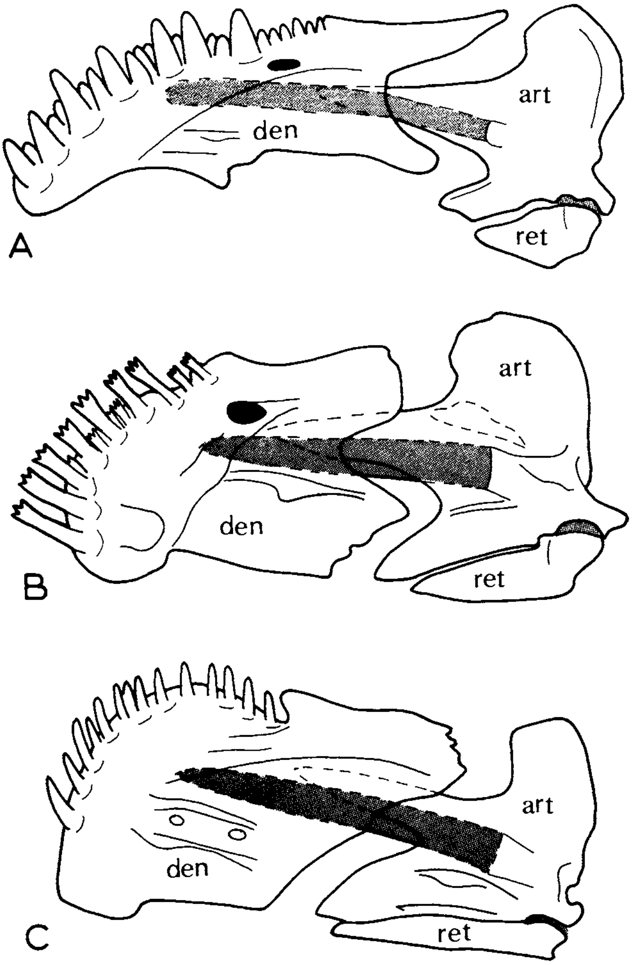

FIG. 38. Diagrammatic representation of lower jaw, lateral view, of A. *Valencia hispanica*; B. *Jenynsia lineata*; C. *Aplocheilichthys johnstoni*. Cartilage is stippled, Meckel's cartilage is elongate medial element.

more expanded, especially at its most anterior end, e.g., in *Procatopus gracilis* (fig. 37). The dentary in this case continues to carry a sensory canal; however, the ossified enclosure of the canal is reduced relative to that in other cyprinodontiforms.

The second division of these cyprinodontoids comprises the genera *Empetrichthys*, *Crenichthys*, *Cubanichthys*, *Chriopeoides*, *Orestias*, the goodeids, and cyprinodontines. The mouth of this group is smaller than that in any other group of cyprinodontiforms. The premaxillary ascending processes are short and attenuate, rather than triangular as in the former group.

In the goodeids and the two North American genera *Empetrichthys* and *Crenichthys*, the dorsal process of the maxilla is present yet weakly formed (fig. 39). The result is a maxilla which has a small cup-shaped process medially to receive the premaxillary ascending process. Because these three taxa share other characters with the more derived cyprinodontiforms, the dorsal process is inferred to be reduced rather than primitively unformed.

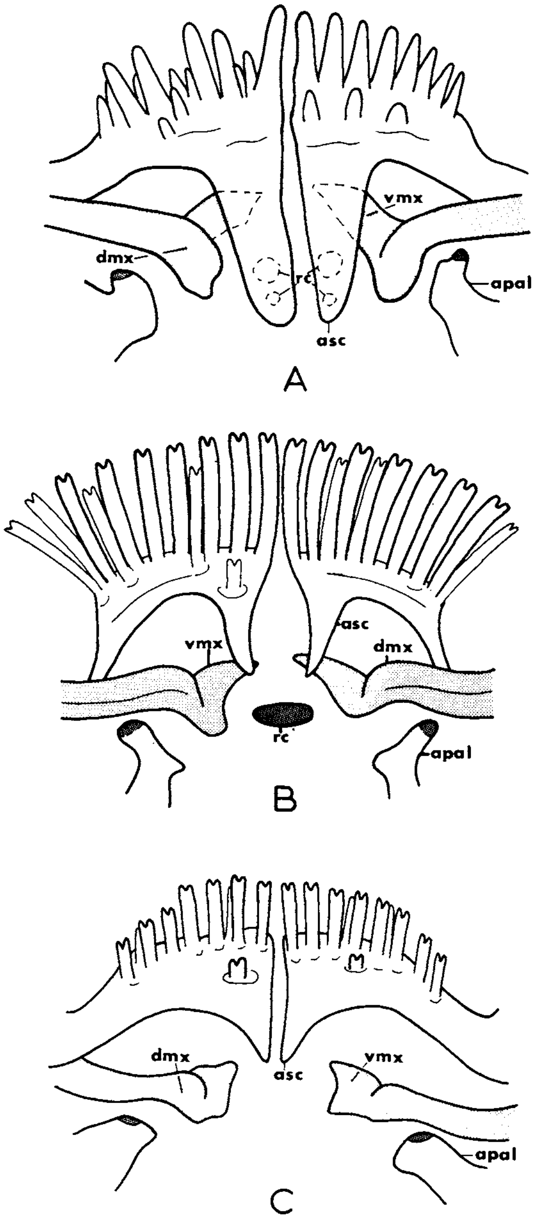

FIG. 39. Diagrammatic representation of the upper jaw in A. *Empetrichthys merriami*; B. *Crenichthys baileyi*; C. *Characodon lateralis*.

Among these three, the distal arm of the premaxilla is straight, rather than S-shaped, although the posterior indentation of the alveolar arm is well-formed (fig. 40).

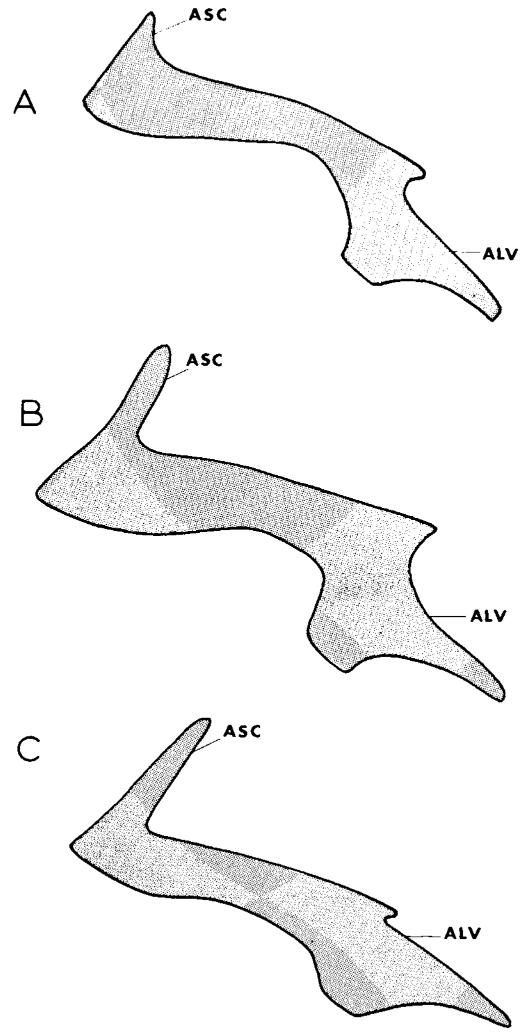

FIG. 40. Diagrammatic representation of premaxilla, lateral view in A. *Characodon lateralis*; B. *Crenichthys baileyi*; C. *Empetrichthys latos pahrump*.

A third unique jaw characteristic of *Empetrichthys*, *Crenichthys*, and the goodeids is the greatly reduced articular that possesses no medial extension to carry the sensory canal (fig. 33B, C, D). A fourth unique character, mentioned previously, is the reduction of the anterior arm of the autopalatine, with no anterior or posterior extensions.

These four jaw and jaw suspensorium characters of goodeids, *Empetrichthys*, and

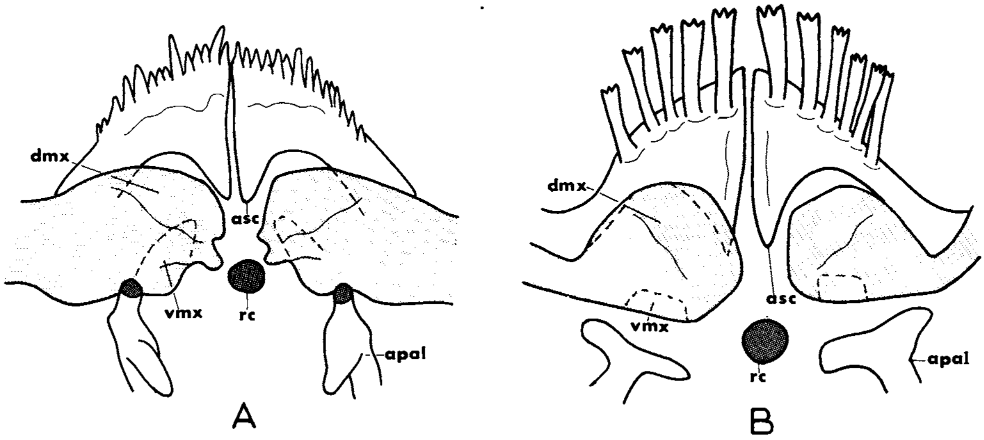

FIG. 41. Diagrammatic representation of the upper jaw in A. *Cubanichthys cubensis*; B. *Aphanius fasciatus*.

*Crenichthys*, along with characteristics of other systems, unite them into a monophyletic group.

In the nominal genera *Cubanichthys*, *Chriopeoides*, *Orestias* and in the cyprinodontines, the dorsal processes of the maxillaries are expanded medially, and nearly meet in the midline (fig. 41). There is also a distinct groove running down the middle of the dorsal process. The large distal arm of the maxilla is correlated in this group (fig. 42) with the development of a robust upper jaw.

*Cubanichthys* and *Chriopeoides* are hypothesized to be the primitive members of this assemblage because they possess two primitive characteristics of the jaws found modified in the remaining members. Both nominal genera possess several rows of teeth on the upper and lower jaw; there is a prominent outer row with smaller, scattered inner jaw teeth not forming regular rows. Also, Meckel's cartilage is narrow posteriorly where it inserts into the medial articular process (e.g., as in fig. 38).

In *Orestias* and the cyprinodontines, the teeth are present in a single outer row on both the upper and lower jaws. These teeth are unicuspid and bicuspid in *Orestias*, unicuspid in *Kosswigichthys*, and tricuspid in remaining cyprinodontines. Teeth occur in a single outer row independently in one other species of cyprinodontiform, the funduline *Lucania parva*.

In addition to a single row of outer teeth, the cyprinodontines and *Orestias* also have a derived lower jaw which is characterized by the posterior expansion of Meckel's cartilage (e.g., as in *Aphanius fasciatus*, fig. 43A). The cartilage is expanded so that it covers a large portion of the articular, in contrast to the state of the cartilage in other cyprinodontiforms (e.g., figs. 27, 38) in which the cartilage is present as a rod of uniform width.

In Anatolian cyprinodontines (e.g., *Aphanius*, fig. 43A) there is a medial extension of the dentary which projects anteriorly. In the South American genus *Orestias* (fig. 43B) the dentary is even further expanded to form a medial shield of bone. The condition in *Orestias* is considered to be the most derived condition of this transition series (i.e., from the typical condition in *Chriopeoides*, fig. 42, to the expanded condition of *Aphanius*, to the fully expanded condition of *Orestias*). The dentary characteristics are correlated with those of the gill arches, shoulder girdle and pattern of squamation, to be discussed. The characteristic lower jaw of these two groups is characterized by a robust dentary and recession of the urohyal and branch-

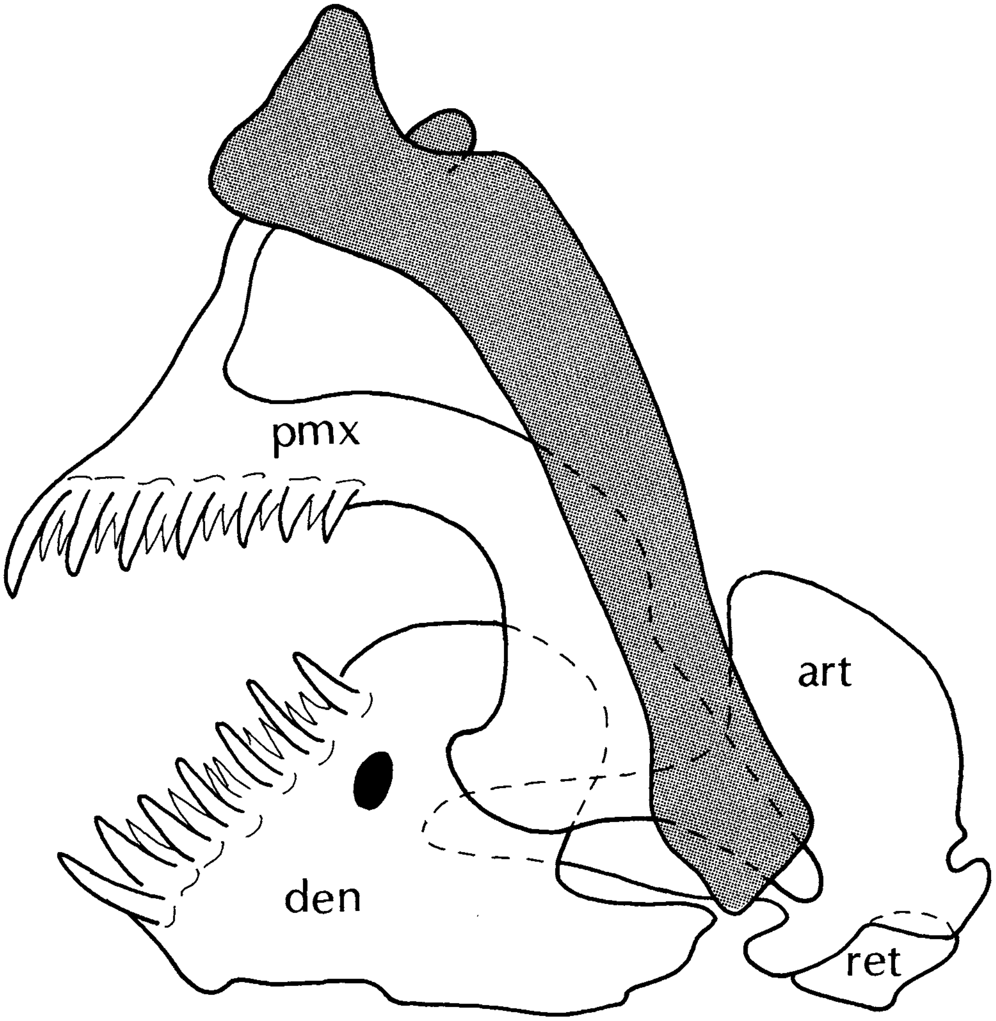

FIG. 42. Diagrammatic representation of upper and lower jaw, lateral view of *Cubanichthys* (*Chriopeoides*) *pengelleyi*.

iostegal rays (fig. 14I). In lateral view, the mouth cleft is nearly vertical (fig. 14G).

*Aphanius fasciatus* has tricuspid jaw teeth, as do other Old World and all New World cyprinodontines. The character transformation series described above for the dentary indicates that if tricuspid teeth can be used as a derived character, it is only at the level of defining the cyprinodontines and *Orestias* as a monophyletic group, with a reversion to unicuspid teeth in some *Orestias* and in *Kosswigichthys*.

Tricuspid outer teeth occur in one other group of cyprinodontiforms, fishes of the genera *Jenynsia*, *Anableps*, and *Oxyzygonectes*. The teeth of *Jenynsia* are distributed in one large outer row and several smaller scattered in indistinct inner rows. All the jaw teeth are tricuspid. However, the shape of the outer teeth of *Jenynsia* varies from distinctly tricuspidate with the inner cusp just slightly longer than the middle (fig. 44B) to a faintly tricuspidate form in which the lateral shoulders are only weakly formed (fig. 44A).

In *Oxyzygonectes* (fig. 36) adults have a

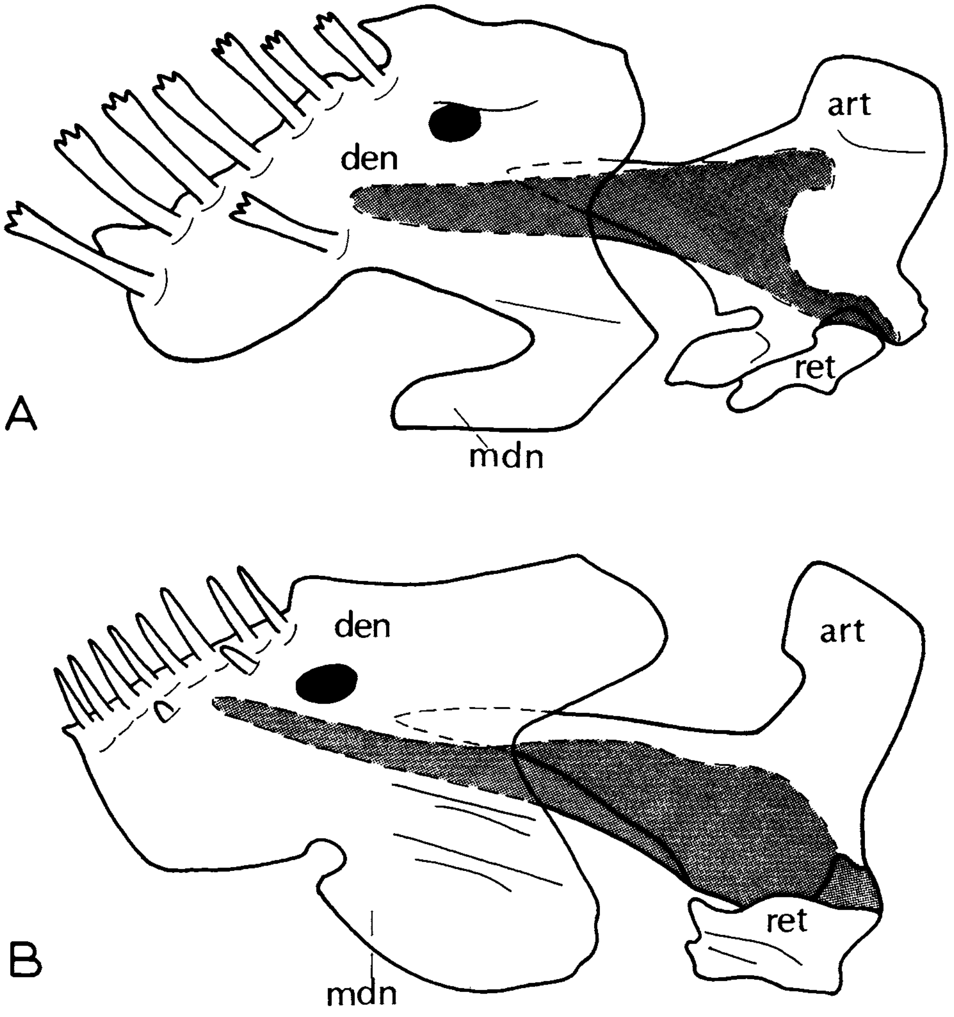

FIG. 43. Diagrammatic representation of lower jaw, lateral view, of A. *Aphanius fasciatus*; B. *Orestias* sp. Cartilage is stippled, Meckel's cartilage is the enlarged medial element.

row of very large recurved unicuspid teeth, and a dense inner patch of teeth which appear to be distributed in about five or six rows. These inner jaw teeth are all tricuspid in both juveniles and adults. The teeth are so closely packed that on a cursory examination they appear to be villiform. The outer teeth of juvenile *Oxyzygonectes* are weakly tricuspidate. Thus, the jaw dentition of *Oxyzygonectes* and *Jenynsia* is apparently very much the same, with *Oxyzygonectes* losing the lateral cusps of the outer row, and having more inner jaw teeth.

The jaw dentition of an adult *Anableps* consists of one large outer row of recurved teeth and several smaller scattered inner rows of unicuspid teeth. The inner jaw teeth have what appear to be weakly formed lateral shoulders.

The upper jaw of an adult *Anableps* is very derived (fig. 35A). There are only weakly formed premaxillary ascending processes and the premaxillaries form an arc. The maxilla is elongated medially, however, the dorsal process of the maxilla and expanded dis-

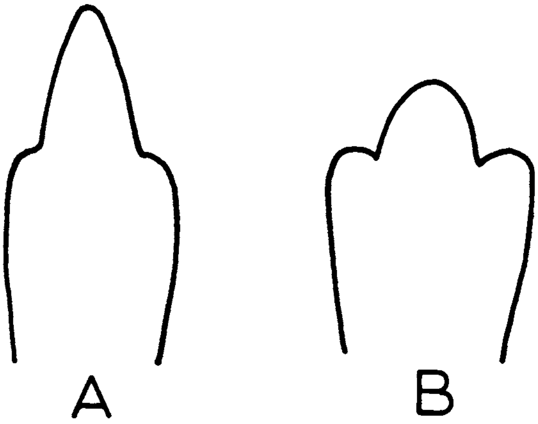

FIG. 44. Sketch of two forms of tricuspid teeth in the genus *Jenynsia* (see text for discussion).

tal arm distinctive of the monophyletic group to which it is assigned are prominent.

Another unique feature is the dumbbell shape of the rostral cartilage, unknown in other cyprinodontiforms. Also, a block of cartilage sits between the autopalatine and the maxilla (fig. 35A) termed here the subautopalatine cartilage. Such a block is often found in this position in atherinomorph fishes; its presence in *Anableps* is therefore considered primitive.

Juvenile *Anableps* show all the specializations of the adults, therefore, an embryo of *Anableps dowi,* the presumed most primitive species of the genus (Miller, 1979) was examined. The yolk sac was removed and the specimen counterstained. The outer teeth of the embryo have distinct lateral shoulders and there is a very narrow medial cusp, they differ little from the weakly tricuspidate teeth in *Jenynsia*. Furthermore, in the embryo, triangular-shaped ascending processes like those in *Jenynsia* and *Oxyzygonectes* are present on the premaxillaries.

Hence, on the basis of dentition, the three genera, *Jenynsia, Anableps,* and *Oxyzygonectes* are hypothesized to form a monophyletic group.

GILL ARCHES: The structure of the branchial skeleton has been used in recent years to deduce phylogenetic relationships because it is both constant within large groups

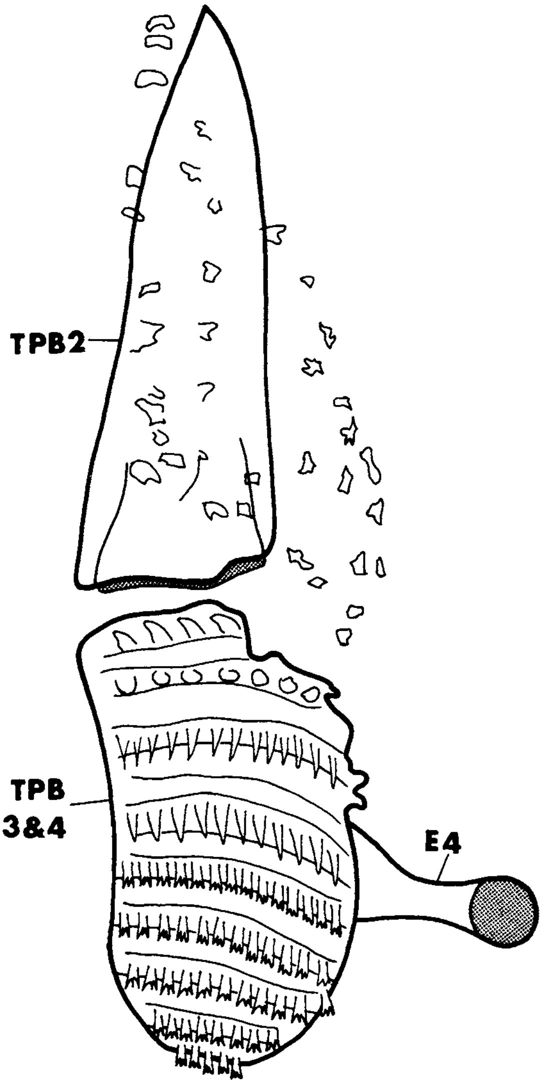

FIG. 45. Diagrammatic representation of dorsal gill arches, ventral view, of *Pantanodon madagascariensis*. Cartilage is stippled.

and quite variable among them (Nelson, 1969; Rosen, 1973). Except in the unusual *Pantanodon* (fig. 45) and certain poeciliids, dorsal gill arch anatomy among cyprinodontoids varies little from the basic structure exhibited by *Profundulus punctatus* (fig. 6B).

In *Profundulus*, the interarcual cartilage is reduced relative to the condition in aplocheiloids. The three pharyngobranchial

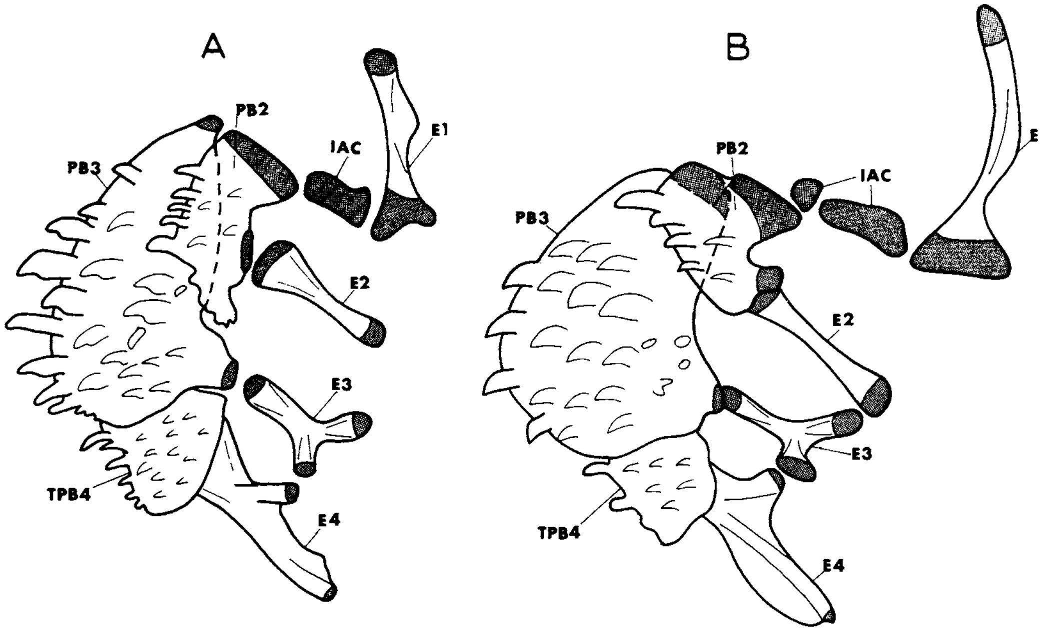

FIG. 46. Diagrammatic representation of dorsal gill arches, ventral view, of A. *Fundulus diaphanus*; B. *Lucania parva*. Cartilage is stippled.

toothplates (associated with pharyngobranchials 2, 3, and 4) are separate elements. The cartilaginous points of articulation are relatively narrow. Species in the subgenera *Zygonectes, Xenisma,* and *Fundulus* of the genus *Fundulus* differ from *Profundulus* in having the cartilaginous point of articulation of the second pharyngobranchial toothplate greatly expanded laterally to produce a broad head for the articulation of the interarcual cartilage (fig. 46A). In the subgenus *Plancterus,* and in the funduline genera *Adinia, Leptolucania* and *Lucania* (fig. 46B), the cartilaginous point of articulation is not enlarged. This is also the case in *Valencia* (fig. 47A) which exhibits the primitive condition for the cyprinodontoids.

Among the more derived cyprinodontoids, the structure of the dorsal gill arches differs most from the general condition in *Pantanodon* and some derived poeciliid genera.

In *Pantanodon madagascariensis* (fig. 45), the second pharyngobranchial toothplate is greatly expanded into a sheet of bone. There are no teeth in sockets on the toothplate; however, toothlike structures lie above it suspended in connective tissue. The third and fourth pharyngobranchial toothplates are fused into one large toothbearing element. The teeth are arranged in discrete rows, with tricuspid teeth being found on the posterior five rows. Epibranchials one through three are absent, as is the interarcual cartilage. (Also, the hypobranchials of *Pantanodon* are reduced or absent, as illustrated by Rosen, 1965.) The expanded second pharyngobranchial toothplate has been found in no other atherinomorph genus examined. Fusion of the third and fourth pharyngobranchial toothplates occurs within a group of cyprinodontines, but otherwise their structure is basically that of the general form.

Among the poeciliids, teeth on the third and fourth pharyngobranchial toothplates are often arranged in discrete rows, and even tricuspid teeth are present. In these poeciliids however, the epibranchials and interarcual cartilage are present, as is a more primitively shaped second pharyngobranchial toothplate. In this study, *Pantanodon* is

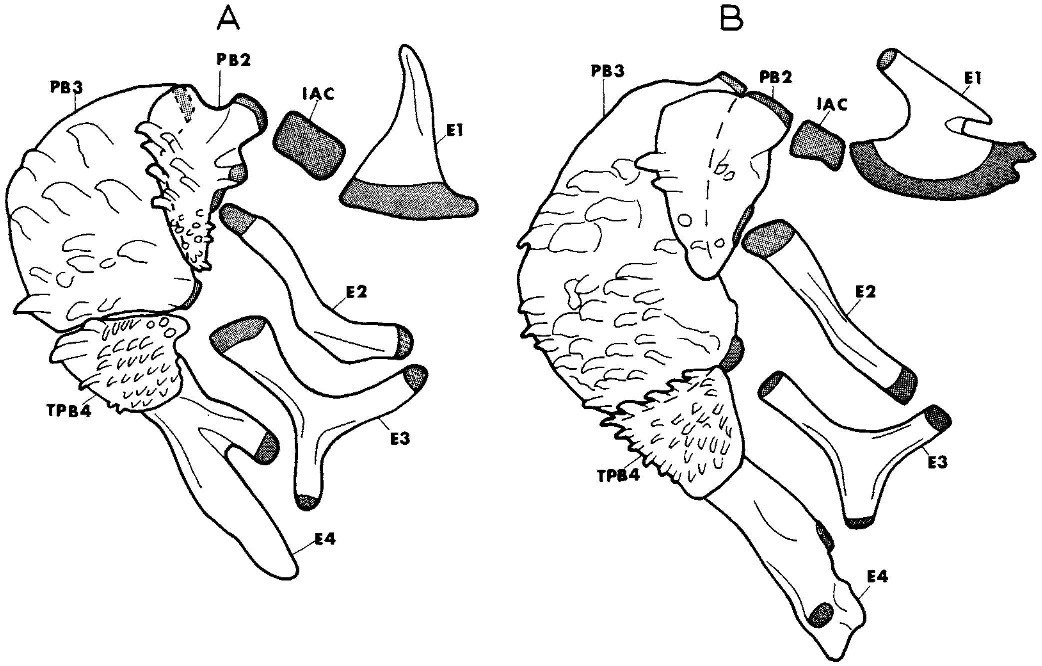

FIG. 47. Diagrammatic representation of dorsal gill arches, ventral view, of A. *Valencia hispanica*; B. *Empetrichthys latos pahrump*. Cartilage is stippled.

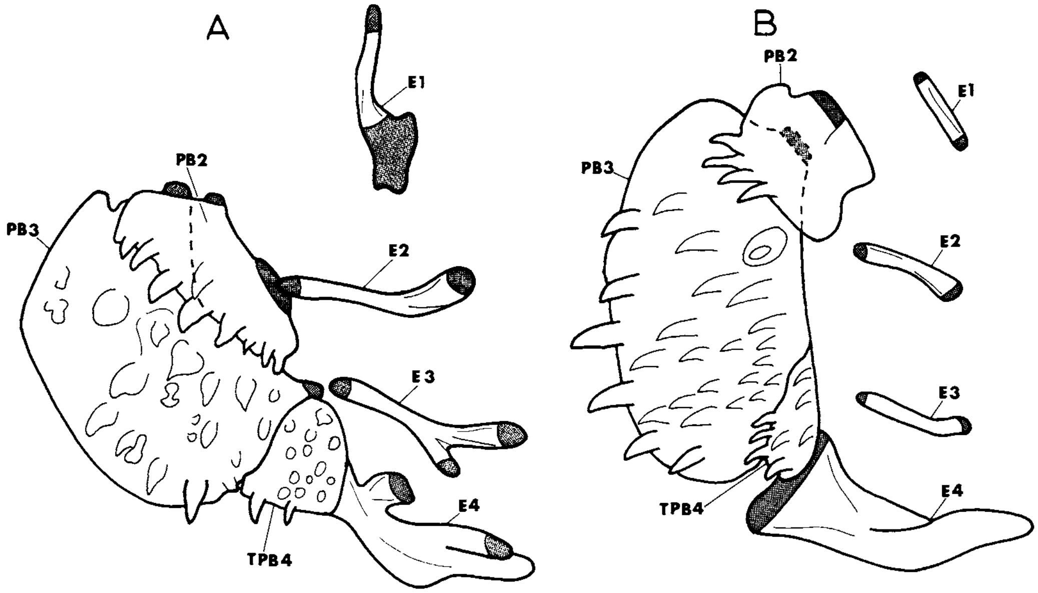

FIG. 48. Diagrammatic representation of dorsal gill arches, ventral view, of *A. Procatopus gracilis*; B. *Tomeurus gracilis*. Cartilage is stippled.

considered to be a close relative of the poeciliids; however, its close relationship is not based on gill arch morphology. *Tomeurus* has dorsal gill arches of the structure primitive for cyprinodontoids (fig. 48B), although the epibranchials are reduced and no interarcual cartilage has been found. These characters are considered derived for the genus, since the cartilage and more robust epibranchials are found in more derived poeciliids. Therefore, either *Pantanodon* is a poeciliid which lost its gonopodium, or the similar gill arch structure of the poeciliids and *Pantanodon* are independently derived. On the basis of the distribution of all derived characters, the latter hypothesis is accepted here.

*Empetrichthys* (fig. 47B) and *Crenichthys* exhibit a peculiar shape of the first epibranchial. The bone is nearly Y-shaped resulting from an indentation at its base. This type of first epibranchial has not been found elsewhere within cyprinodontiforms.

In the cyprinodontines and *Orestias*, the second pharyngobranchial is offset to the third, as in *Cyprinodon variegatus* (fig. 49). This change in orientation of the pharyngobranchial excludes the cartilaginous point of articulation from the ventral toothed surface of the pharyngobranchial toothplates. In addition, the fourth pharyngobranchial toothplate is reduced. However, such a reduction is not unique to this group, as the toothplate is also reduced in *Procatopus* (fig. 48A) and other procatopines.

In *Cyprinodon* (fig. 49) the third and fourth pharyngobranchial toothplates are fused into a single toothbearing element. The teeth are arranged in rather discrete rows. Such fusion occurs in many, perhaps most, individuals of the New World cyprinodontine genera *Cyprinodon, Jordanella, Garmanella, Megupsilon, Floridichthys,* and *Cualac,* and in *Orestias*. Although the occurrence of some individuals with unfused toothplates makes the upper pharyngeal character difficult to use, the regular arrangement of the teeth is a constant defining character of all of these genera.

In *Floridichthys carpio* (fig. 50A) there is a distinct first pharyngobranchial cartilage as well as a toothplate which bears a patch of teeth. In *Cualac tessellatus* (fig. 50B) there is no toothplate yet there is a distinct separate cartilage which sits at the anterior tip of the first epibranchial cartilage.

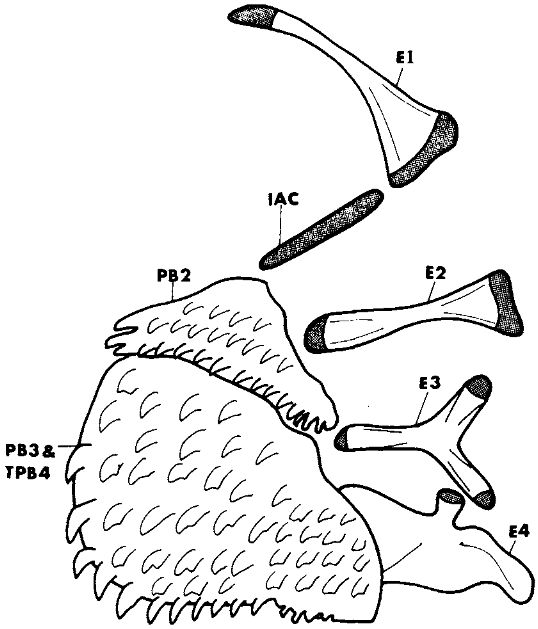

FIG. 49. Diagrammatic representation, dorsal gill arches, ventral view, of *Cyprinodon variegatus*. Cartilage is stippled.

An element in this position has been found in only one other species of cyprinodontiform, *Cynolebias elongatus*. In this Neotropical aplocheiloid, there is a distinct cartilage as well as a bony toothbearing element. Its condition is comparable to that of *Floridichthys*.

Among atherinomorph fishes, no first pharyngobranchial toothplate is found except in the genera *Cynolebias* and *Floridichthys*. An ossified first pharyngobranchial is present among some atherinoid fishes, including species of the genera *Melanotaenia* and *Menidia*. Otherwise among atherinomorphs, first pharyngobranchial elements are absent. Their appearance within these two rather unrelated groups of cyprinodontiforms poses a problem for interpretation. If the condition is a retained primitive character, then the most parsimonious interpre-

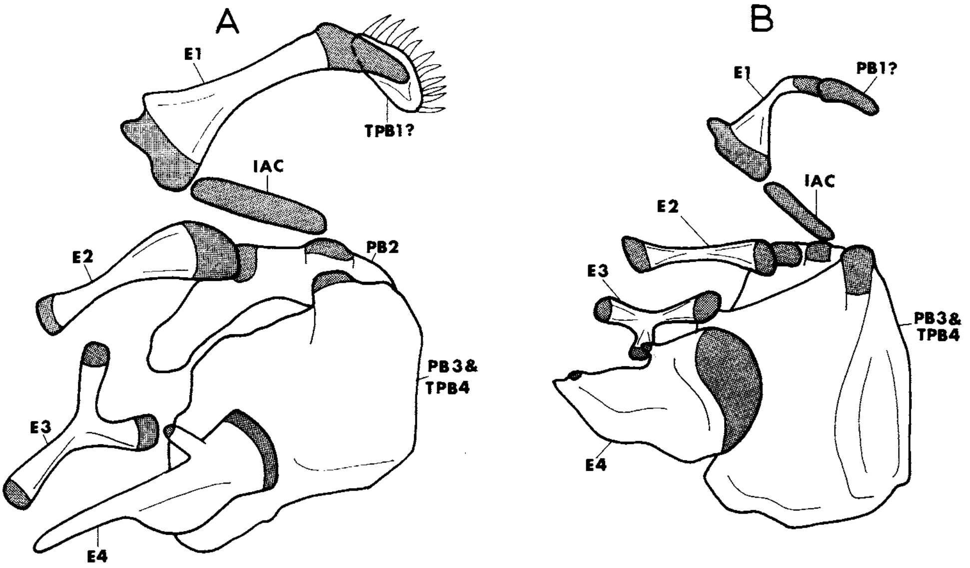

FIG. 50. Diagrammatic representation of dorsal gill arches, dorsal view, of A. *Floridichthys carpio*; B. *Cualac tessellatus*. Cartilage is stippled.

tation in light of all other data would be that the elements are lost individually in all other groups of cyprinodontiforms. So many independent losses, however, presuppose far more evolutionary events than if it is assumed that these elements are uniquely derived twice among cyprinodontiforms, once in *C. elongatus* and again in *Floridichthys* and *Cualac*, thereby supporting a sister group relationship of the last two genera. The condition may also define a subgroup of *Cynolebias* species.

PECTORAL GIRDLE: The pectoral fins of cyprinodontiforms are described as typically lowset, with the corresponding radials situated ventrally rather than dorsally. There is a large, scale-shaped first postcleithrum and a thin third postcleithrum. The posttemporal may have an ossified lower limb, or a limb represented solely by a ligament; this character is used only at the lower levels of phylogeny reconstruction since it is not correlated with larger sets of characters used to delimit major groups.

Shoulder girdles are lowset in all cyprinodontiforms except the poeciliids, *Fluviphylax, Pantanodon,* and the procatopines. Within this group, the pectoral fins are distinctly highset (e.g., as in *Tomeurus gracilis*, fig. 51; and *Heterandria bimaculata*, fig. 52; and the procatopines *Procatopus glaucicaudus*, fig. 53) as opposed to the lowset fins of, for example, *Rivulus* (fig. 54), *Cualac* (fig. 55) and *Lucania* (fig. 56). The highset pectoral fins are related to the placement of the radials in a dorsal position on the scapulocoracoid, and a gently arched dorsal limit of the scapula and cleithrum (fig. 8C, D). This is correlated with a loss of the first postcleithrum which is wanting in all members of the group except for some nominal species of the genus *Aplocheilichthys*. The structure of the shoulder girdle of *Profundulus* (fig. 8A) is the general condition, as in the aplocheiloids with the radials situated ventrally.

The pectoral fins are distinctly lowset in the genera *Anableps, Jenynsia,* and *Oxyzygonectes*, as well as other cyprinodontiforms; however, as stated, the pectoral fins are generally highset in most other groups of atherinomorph fishes. Since the derived form of the pectoral fins has been interpreted as lowset within cyprinodontiforms, the highset pectoral fins may only be interpreted as sec-

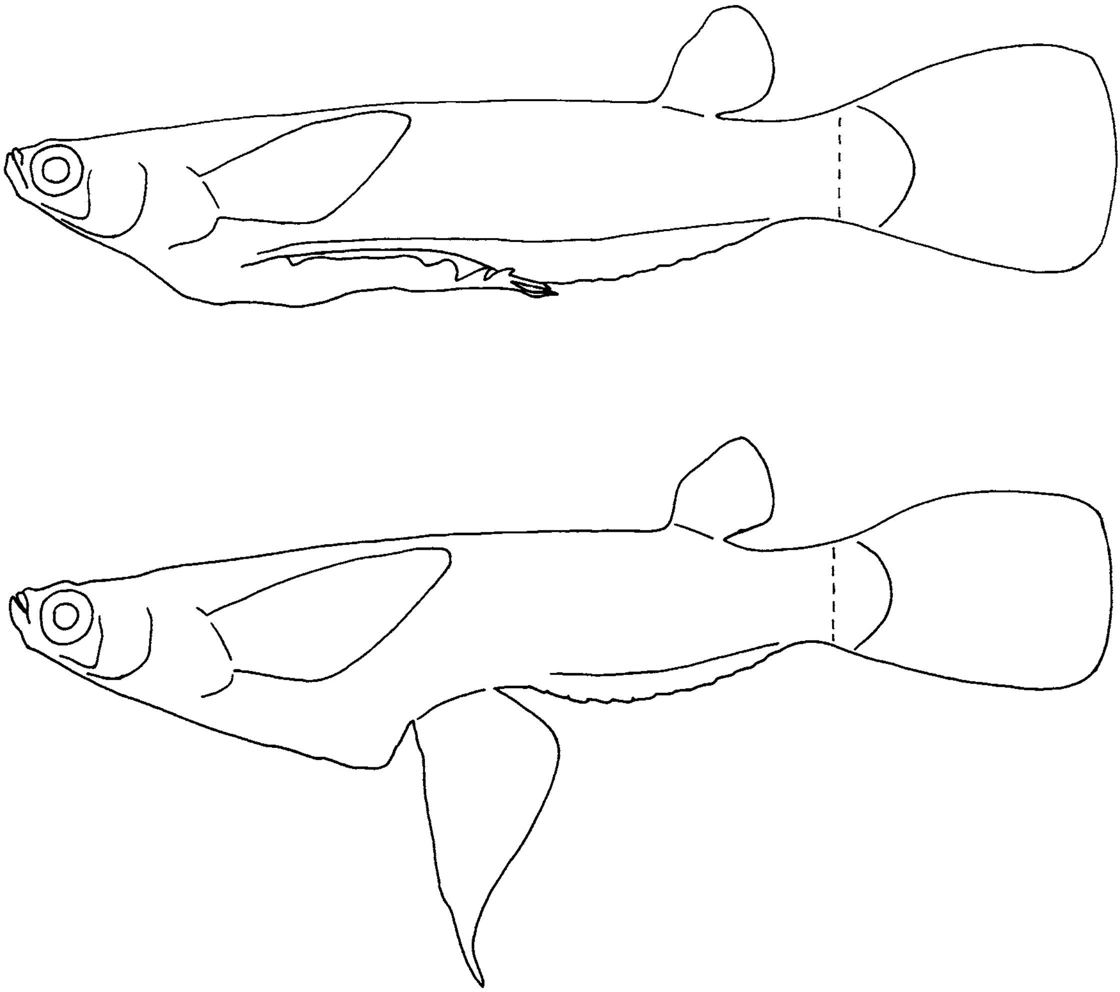

FIG. 51. Sketch of body form and fin position of *Tomeurus gracilis*, male above, female below. Dotted line approximates base of hypural plate. (After Rosen and Bailey, 1963.)

ondarily derived in poeciliids, procatopines, *Pantanodon* and *Fluviphylax*.

SKULL ANATOMY: A constant feature of the skull of aplocheiloids is the presence of a lateral facet on the anterior surface of the lateral ethmoid which articulates with the head of the autopalatine (fig. 17). Such an extension is present in the cyprinodontoids only in the genus *Profundulus* (fig. 57A). This character was one of several Farris (1968) used to separate the species of *Fundulus* from *Profundulus*; he reported the process as absent in all species of *Fundulus* examined. The presence of this character in all aplocheiloids and *Profundulus* suggests that it is a primitive character for cyprinodontiforms. Thus, its absence or reduction in all other cyprinodontoids is evaluated as a derived character supporting their monophyly.

The generalized state of the size and position of the lateral ethmoid is exemplified by *Tomeurus gracilis* (fig. 16B).

Among procatopines, the lateral ethmoid is expanded medially under the broad arm of the parasphenoid, as in *Aplocheilichthys johnstoni* (fig. 16C). (Compare this expan-

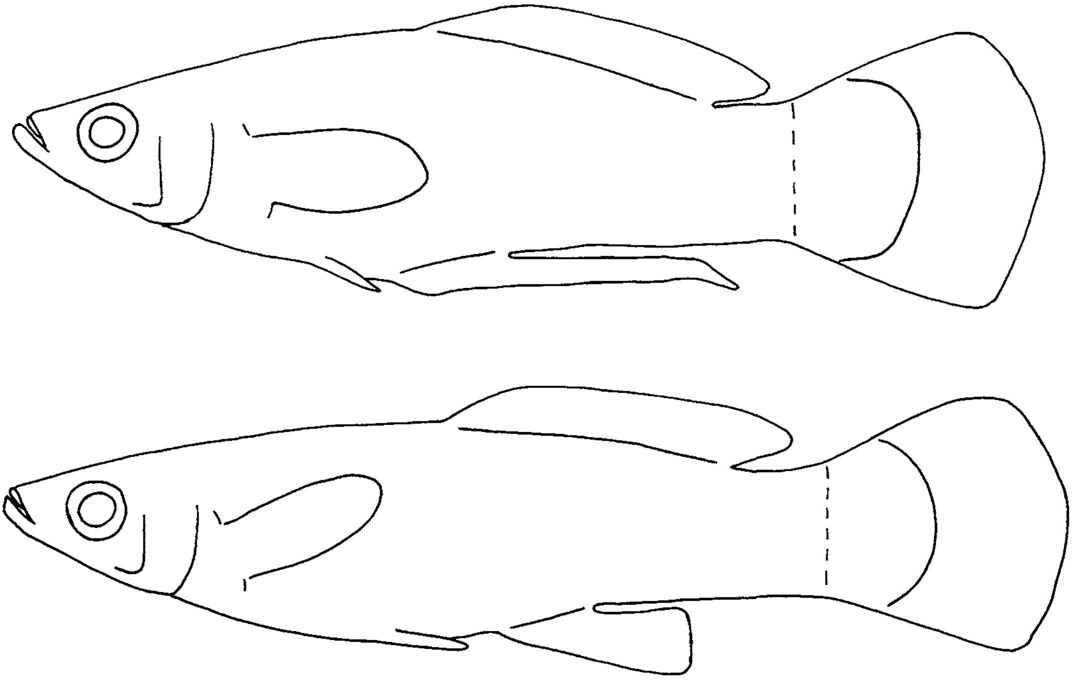

FIG. 52. Sketch of body form and fin position of *Heterandria bimaculata*, male above, female below. Dotted line approximates base of hypural plate. (After Rosen, 1979.)

sion of the lateral ethmoid with that of the Neotropical aplocheiloids, fig. 17C.)

Medial expansion of the lateral ethmoid is accompanied by a change in its orientation relative to the frontal bones in *Empetrichthys*, *Crenichthys*, the goodeids, *Cubanichthys*, and *Chriopeoides*, the cyprinodontines and *Orestias*. As in the goodeid, *Characodon lateralis* (fig. 57D), the lateral ethmoid is oriented such that the greater part of the element lies anterior to the limit of the frontals. This may be compared with the general condition in cyprinodontoids as in *Profundulus punctatus* (fig. 57A), in which the outer flange of the lateral ethmoid is expanded, rather than narrow as in *Characodon*.

Among the fundulines, the lateral ethmoid is also expanded under the parasphenoid (fig. 16A). However, the lateral ethmoid not only lacks the facet for articulation of the autopalatine, but the autopalatine does not come in contact with the lateral ethmoid. Rather, the fundulines' pronounced snout is effected not only by the anteriorly projecting ventral arms of the maxillaries, but by the extension of the autopalatines to a position lateral to the enlarged vomer as well.

The mesethmoid is cartilaginous in aplocheiloids. In addition, it is cartilaginous among the cyprinodontoids in *Pantanodon* and the procatopines (it is ossified in *Fluviphylax*) as well as in the Anatolian cyprinodontines. The cartilaginous mesethmoid is considered a derived condition defining the aplocheiloids; among the cyprinodontoids, its independent occurrence within two unrelated groups is convergent.

The group consisting of *Empetrichthys*, *Crenichthys*, the goodeids, *Cubanichthys*, and *Chriopeoides*, the cyprinodontines and *Orestias* possess another derived feature of the skull; viz., a reduced autopterotic fossa (fig. 57B, C, D). Uyeno and Miller (1962) used the narrow fossa to separate *Empetrichthys* and *Crenichthys* from *Profundulus* which has an extremely wide fossa (fig. 57A).

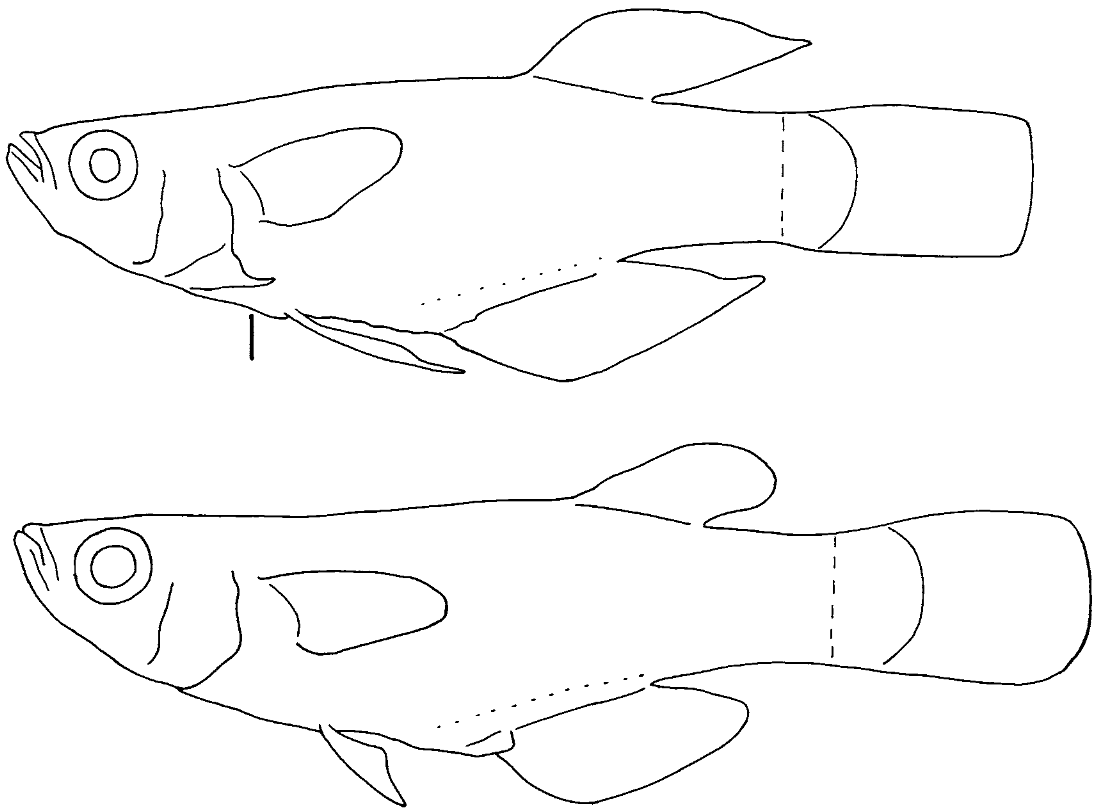

FIG. 53. Sketch of body form and fin position of *Procatopus glaucicaudus*, male above, female below. Dotted line approximates base of hypural plate. (After Clausen, 1959.)

However, they did not compare this condition to its state in other cyprinodontiforms. The fossa of *Profundulus* is wider than in any other cyprinodontiform and may be considered an autapomorphy of the genus.

Enlarged supraoccipital and epiotic processes occur among many groups of acanthopterygian fishes. The general condition of the supraoccipital crests among atherinomorph fishes is paired (Rosen, 1964); among cyprinodontiforms this is the case except in the two monotypic genera *Cubanichthys* and *Chriopeoides*. In these genera the supraoccipital crest is a large, single process which extends above the dorsal profile (fig. 58). Thus, the sister group relationship of these two genera is supported again.

Another unique form of the supraoccipital processes is shared by *Anableps*, *Oxyzygonectes* and *Jenynsia*. As illustrated for *Oxyzygonectes dowi* (fig. 59) the crests are greatly elongate and are separated by a distinct notch from the dome over the foramen magnum. In contrast, supraoccipital crests are present in *Profundulus* (fig. 60), yet they abut the dorsal wall of the foramen magnum, rather than being separated from it by a notch.

The states of the first vertebra in oviparous cyprinodontiforms have been described, although somewhat erroneously, by Sethi (1960). All the aplocheiloids have a complete neural spine on the first vertebra (fig. 26). Among the cyprinodontoids, the neural arch of the first vertebra is open, and therefore, does not form a neural spine (fig. 60) in *Profundulus*, *Valencia*, *Empetrichthys*, *Crenichthys*, the fundulines, and goodeids.

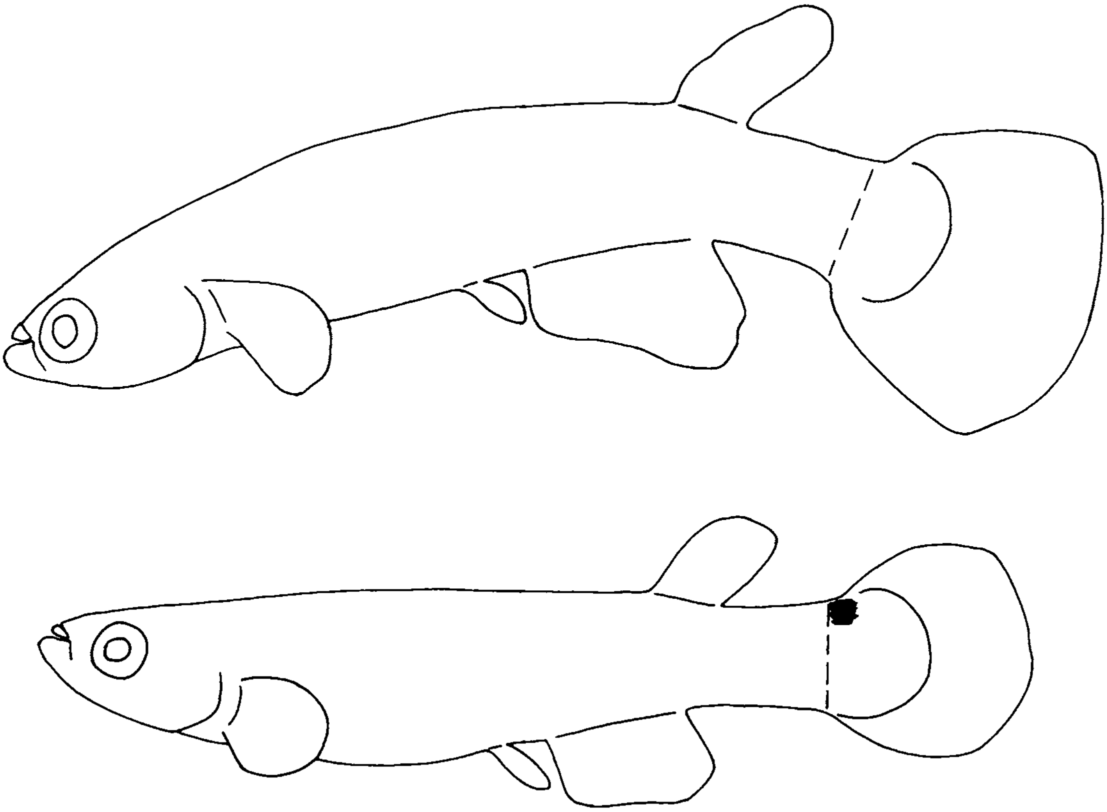

FIG. 54. Sketch of body form and fin position of *Rivulus beniensis,* male above, female below. Dotted line approximates base of hypural plate. (After Klee, 1965.)

Among the procatopines, as well as in *Fluviphylax,* the neurapophyses meet in the midline; no distinct spine is formed, however. The condition is interpreted as a reduction in the neurapophyses and a secondarily derived medial fusion. In this group as well as in the aforementioned cyprinodontiforms, the basioccipital and exoccipital condyles are all well-formed.

In all poeciliids, as well as *Pantanodon,* there are no exoccipital condyles. The attachment of the first vertebra to the skull in *Tomeurus* (fig. 61) involves the forward expansion of the neurapophyses around the base of the foramen magnum. The arch is open and the first vertebra articulates with the skull only via the basioccipital condyle.

In *Pantanodon,* as well as some of the more derived poeciliids such as those of the genus *Poecilia,* the neurapophyses are even more expanded anteriorly and applied to, and fused with, the skull. This characteristic attachment of the first vertebra must be considered independently derived in both *Pantanodon* and the poeciliids if the monophyly of the poeciliids based on the presence of a gonopodium and other reproductive specializations is accepted.

A superficially similar condition of the attachment of the first vertebra to the skull occurs in the New World cyprinodontines of the nominal genera *Cyprinodon, Megupsilon, Jordanella, Floridichthys, Cualac,* and *Garmanella.* There is no spine formed by the neurapophyses of the first vertebra. Instead, the neurapophyses are slightly expanded, brought forward, and applied to the skull (fig. 62). The exoccipital condyles are lacking

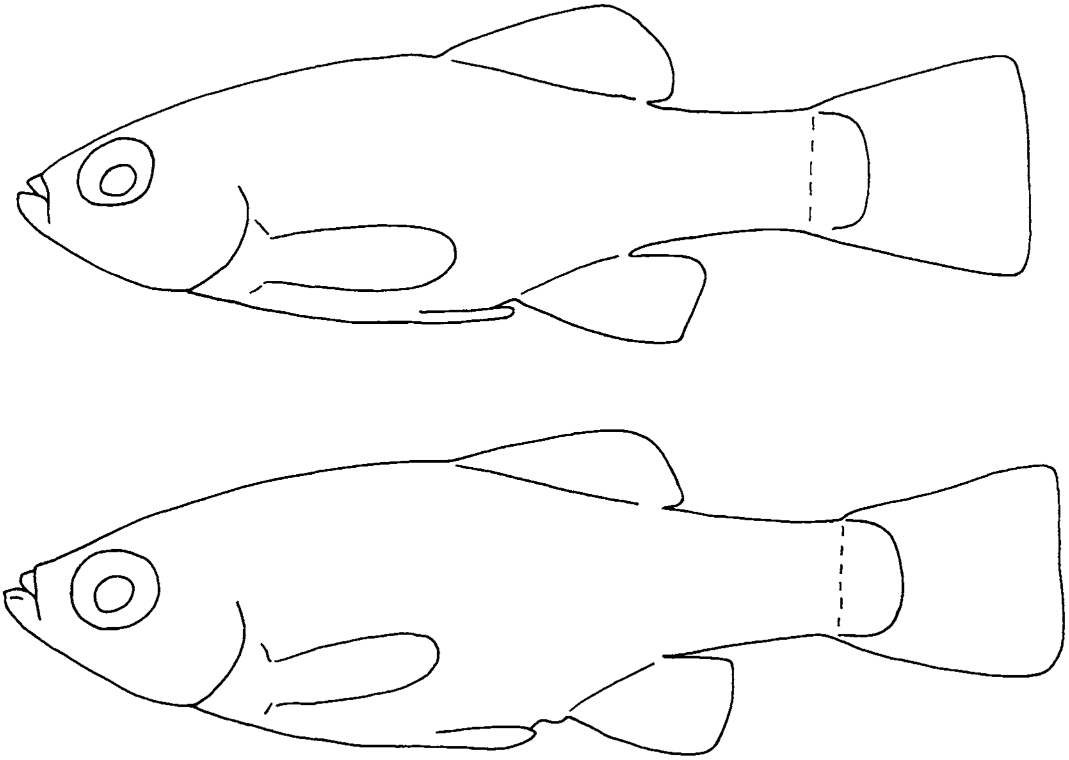

FIG. 55. Sketch of body form and fin position of *Cualac tessellatus*, male above, female below. Dotted line approximates base of hypural plate. (After Miller, 1956.)

and, in addition, the supraoccipital forms the roof of the foramen magnum. In all other cyprinodontiforms, as well as in the poeciliids and *Pantanodon,* the supraoccipital is excluded from formation of the foramen magnum. Also, the form and position of the neurapophyses is quite different between the poeciliids and New World cyprinodontines. In poeciliids, they are greatly expanded and form a trough in which the supraoccipital region of the skull sits; in cyprinodontines, the neurapophyses are simply applied to the skull and provide reinforcement yet form no trough similar to that of the poeciliids.

In *Orestias* and the Anatolian cyprinodontines the exoccipital condyles are present as in *Profundulus,* yet reduced. The neurapophyses of the first vertebra are also reduced, as in the New World cyprinodontines, and may or may not meet in the midline.

The vomer is absent in *Pantanodon, Fluviphylax,* the procatopines (except *Poropanchax, Lamprichthys* and species of *Aplocheilichthys*), and the South American *Orestias.* The vomer is hypothesized to be lost independently at least twice among cyprinodontiforms, once in *Orestias,* and once in the procatopines, *Fluviphylax* and *Pantanodon.* The significance of its distribution is discussed in the following section.

Parietals are absent in two groups of cyprinodontoids. They are lacking in *Orestias* and the cyprinodontines, as well as the procatopines, *Fluviphylax* and *Pantanodon.* Their absence in these two groups is considered to be an independent loss. In addition, their absence from more derived members of the poeciliids is secondarily derived since parietals are present in *Tomeurus.*

Axial Skeleton: The first pleural rib arising on the parapophyses of the second vertebra

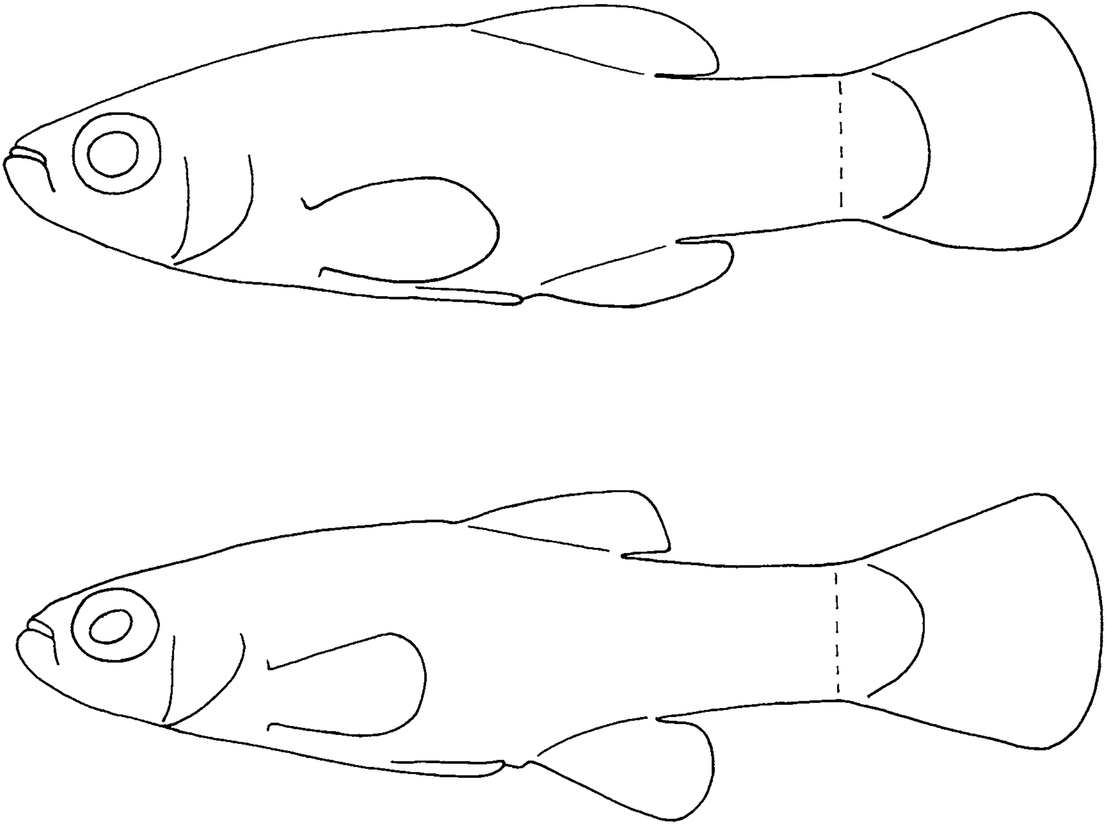

FIG. 56. Sketch of body form and fin position of *Lucania parva*, male above, female below. Dotted line approximates base of hypural plate. (After Hubbs and Miller, 1965.)

has been described as a derived character of cyprinodontiforms. This state occurs in all members of the group except the funduline genus *Adinia* in which the rib arises on the parapophyses of the first vertebra. Since the general state among acanthopterygians is for the rib to be on the third vertebra, this case in *Adinia* is hypothesized to be a further derived state in the transition series, and serves as a defining character of the genus.

The parapophyses themselves are generally robust, with the pleural rib inserting into a furrow in the posterior face of the process. Within *Orestias* and the cyprinodontines, the transverse processes are reduced to cup-shaped processes (Sethi, 1960) into which the pleural ribs insert. This reduction is considered as another derived character of *Orestias* and the cyprinodontines.

Pleural ribs by definition occur only on parapophyses of abdominal vertebrae and not on caudal vertebrae. However, within *Pantanodon*, the procatopines and some poeciliids including *Xiphophorus* and *Poe-*

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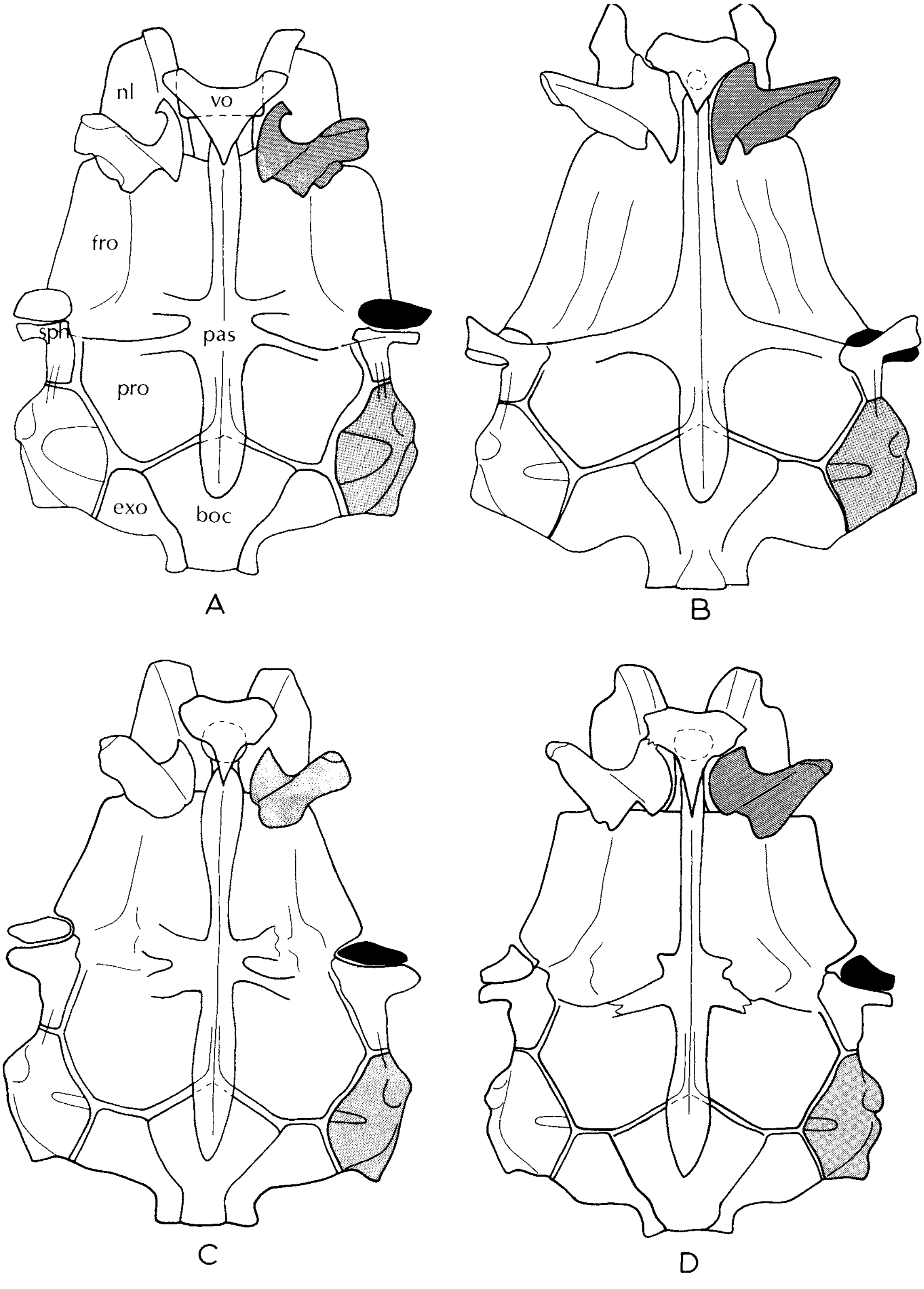
FIG. 57. Diagrammatic representation of the skull, ventral view, in A. *Profundulus punctatus*; B. *Cyprinodon variegatus*; C. *Empetrichthys latos pahrump*; D. *Characodon lateralis*. Lateral ethmoid is cross-hatched; lacrimal is blackened; autopterotic stippled.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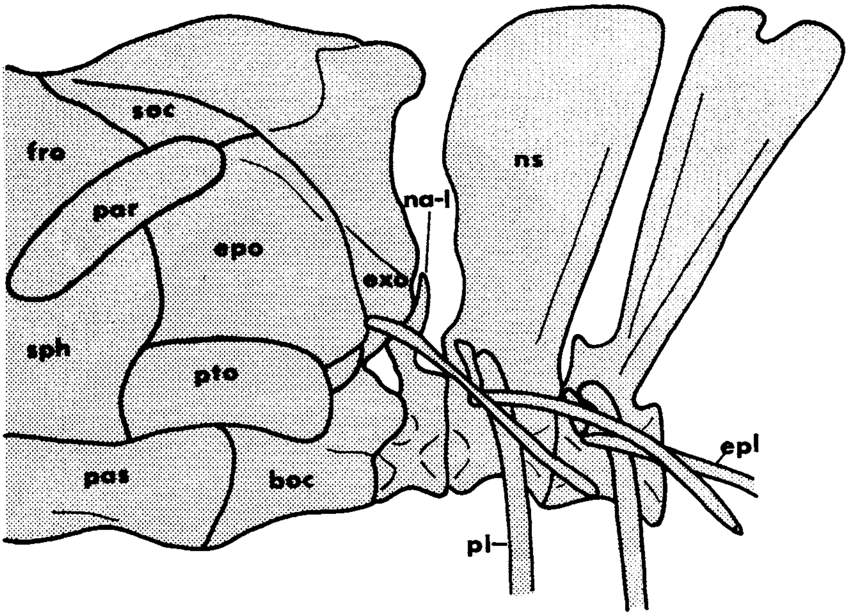

FIG. 58. Diagrammatic representation of the posterior region of the skull and attachment of first vertebra, lateral view, of *Cubanichthys* (*Chriopeoides*) *pengelleyi*. Posttemporal removed.

*cilia*, at least one or two pleural ribs are found on the first and second caudal vertebrae. This character, absent in *Fluviphylax* and certain poeciliids, is ambiguous.

Sensory Pores and Cephalic Squamation: The general pattern of the head scales and sensory pore patterns of cyprinodontiform fishes is exhibited by the genus *Jenynsia* (fig. 14B). There are seven preorbital, three or four lacrimal, four mandibular, and six or seven supraorbital pores.

In *Jenynsia*, there is a break between the anterior and posterior section of supraorbital pore 2, termed 2a and 2b. A series of three pores (2b, 3, and 4) follow the section formed by pores 1 and 2a. There is another break between sections of pore 4 referred to as pores 4a and 4b. The section 4b through 7 completes the supraorbital series. Gosline (1949) figured an identical pattern for *Fundulus chrysotus* and stated that this was the common pattern among *Fundulus* species. It was also observed that such a pattern is typical of cyprinodontoids such as *Profundulus* (also reported by Miller, 1955a), *Oxyzygonectes*, and many but not all goodeids (see Miller and Fitzsimons, 1971). In *Anableps*, the central row of pores (2b through 4a) is reduced to two pores which are referred to as pores 3 and 4a. Departure from the general squamation pattern also occurs in *Anableps* in which there are many scales arranged in a scattered pattern which cannot readily be interpreted using Hoedeman's terminology.

Since the pattern of *Jenynsia* is postulated as the plesiomorphic sensory pore pattern, departures from this pattern are of interest in defining monophyletic groups of cyprinodontoids. However, patterns discussed here are only the most common ones found within a group of genera. A rigorous analysis of head pore and scale patterns requires a survey of inter- and intraspecific variation that is outside the scope of this study.

Supraorbital pores of the poeciliids, procatopines, *Fluviphylax* and *Pantanodon* show an apparently unique modification. The maximum development of sensory pores of poeciliids (fig. 14D, E, F) was based on a

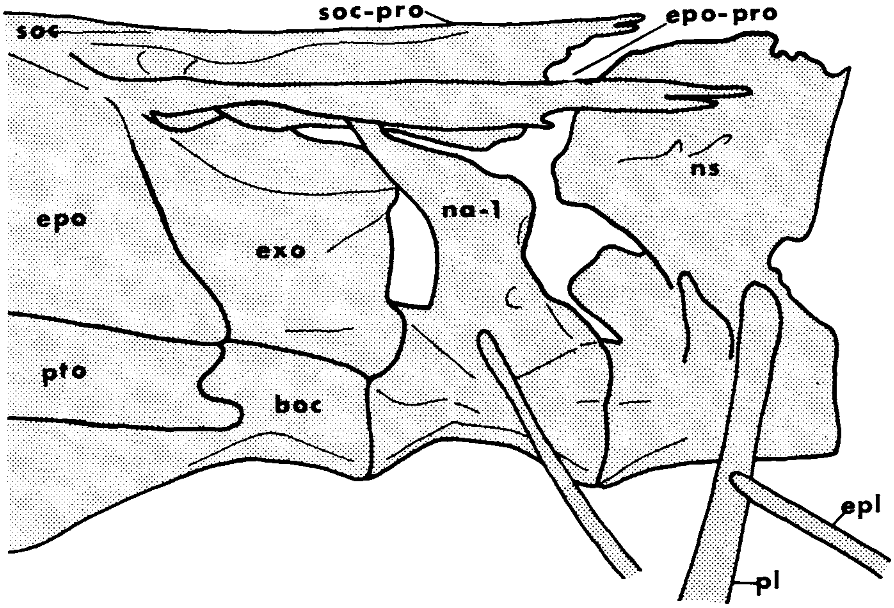

FIG. 59. Diagrammatic representation of the posterior region of the skull and attachment of first vertebra, lateral view, of *Oxyzygonectes dowi*. Posttemporal removed.

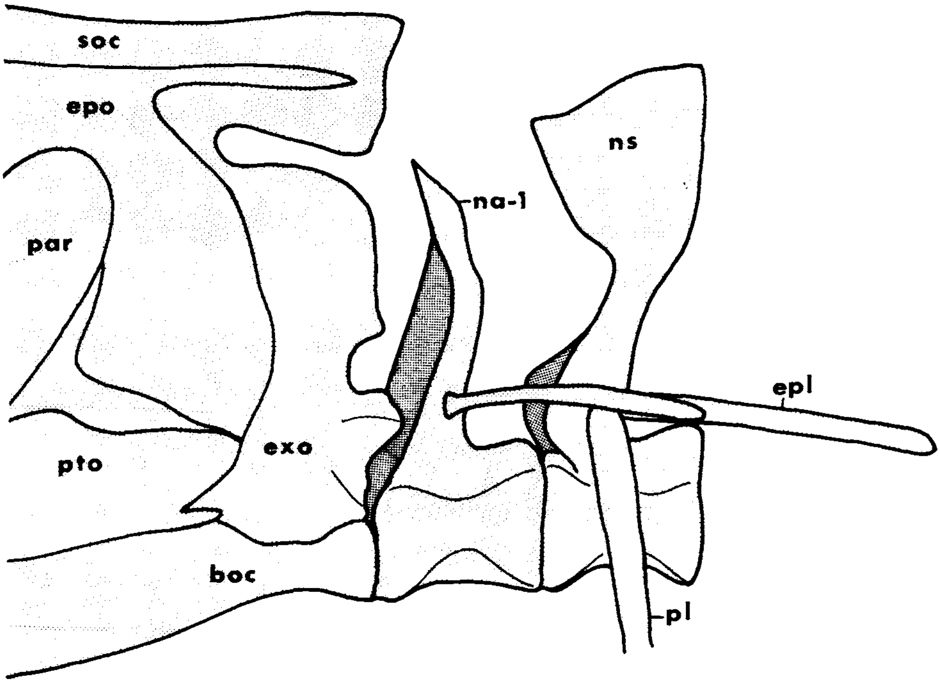

FIG. 60. Diagrammatic representation of the posterior region of the skull and attachment of first vertebra, lateral view, of *Profundulus punctatus*. Posttemporal removed.

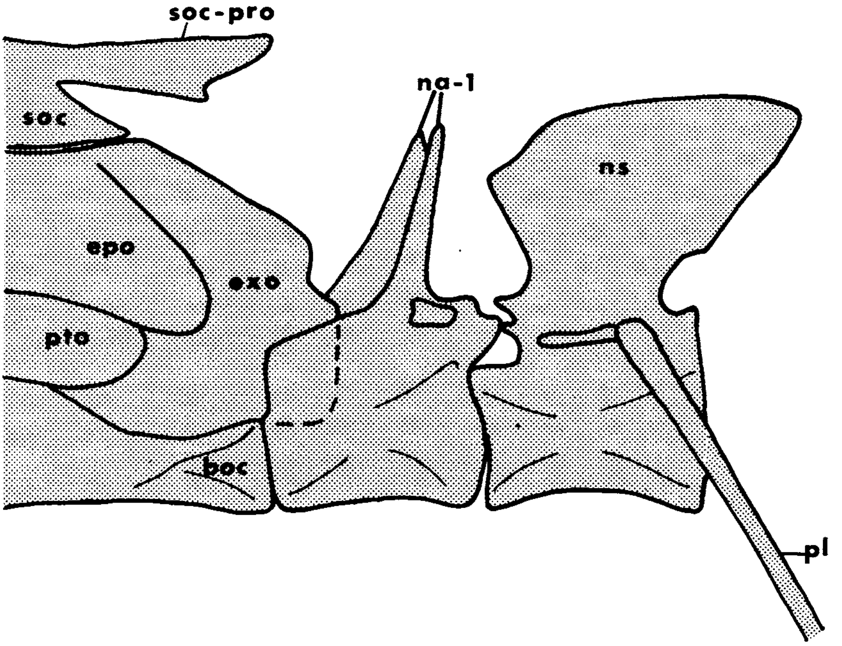

FIG. 61. Diagrammatic representation of the posterior region of the skull and attachment of first vertebra, lateral view, of *Tomeurus gracilis*. Posttemporal removed.

survey of such patterns in all major supraspecific categories of the family (Rosen and Mendelsohn, 1960). The supraorbital pores lie in groupings similar to the plesiomorphic pattern for cyprinodontiforms. The unique feature is the recessed neuromasts in the middle section (pores 2b through 4a) forming a small trough. (*Poropanchax* was defined on the basis of its embedded neuromasts which open as a series of pores.) The pattern is only weakly shown by the diminutive *Fluviphylax* and by *Pantanodon*.

The connection of the canal between pores 4a and 4b (forming just one pore 4) occurs in *Empetrichthys* and *Crenichthys*, both of which retain the disrupted canal between pores 2a and 2b.

The pattern Gosline termed the simplest among cyprinodontiforms (in the cyprinodontines *Cyprinodon, Floridichthys,* and *Garmanella,* and the funduline *Lucania*) in addition to connection of canals between 4a and 4b involves a connection between 2a and 2b (resulting in one pore 2). Thus, the canal is continuous between pores 1 through 7.

In the New World cyprinodontine *Jordanella* and some goodeids (see Gosline, 1949), the canal is continuous except for a break between pores 4a and 4b. This pattern is considered to be independently derived in *Jordanella* and among a group of goodeids.

Reduction of the pore system to pores 6 and 7 only, occurs in the fundulines *Adinia* and *Leptolucania*. A cephalic sensory pore system is absent in the monotypic New World cyprinodontine, *Megupsilon*.

In *Cubanichthys* a canal is present between what appear to be pores 1 and 3 only, although Gosline stated they were present between pores 2 and 3 as well as 6 and 7. There are no pores posterior to what is identified here as pore 3 in *Cubanichthys*; however, since Gosline reports pores 6 and 7 present they must be considered part of the maximally developed pattern. Because of their position, I interpret the first two pores as 1 and 3, even though by definition the pore anterior to 3 should be 2b or 2. The ambiguity of the numbering system is evident in such a case.

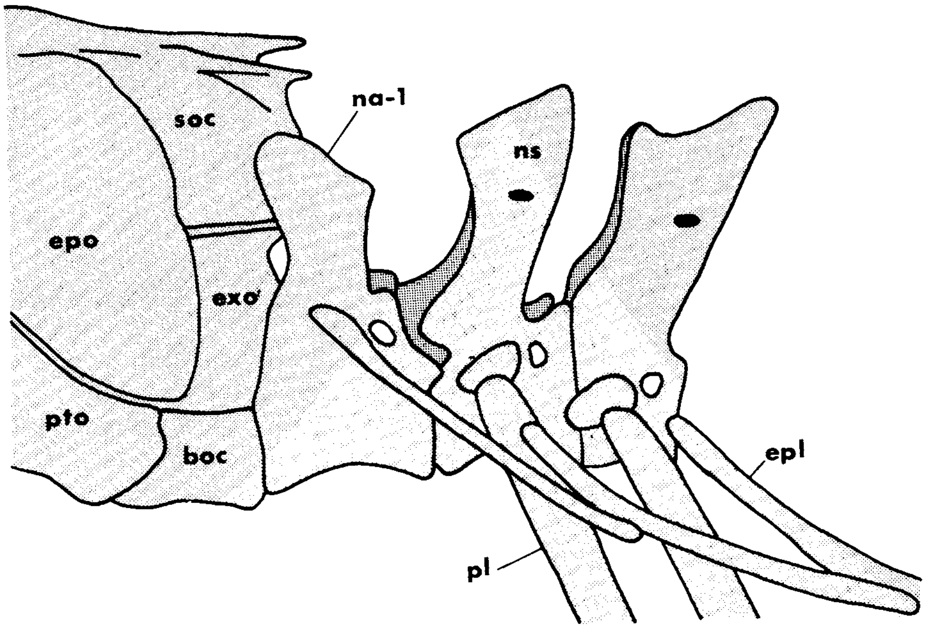

FIG. 62. Diagrammatic representation of the posterior region of the skull and attachment of first vertebra, lateral view, of *Cyprinodon variegatus*. Posttemporal removed.

Pore 3 of *Cubanichthys* is large, as it is in *Chriopeoides*, and is considered a synapomorphy of the two monotypic genera.

Replacement of the two E scales by one large E scale also occurs within the New World cyprinodontines, *Lucania, Cubanichthys, Chriopeoides, Empetrichthys*, and *Crenichthys*. Reduction of the number of pores is apparently correlated at some level with the reduction in the number of head scales.

Gosline reported that *Aphanius dispar*, an Anatolian cyprinodontine, has a canal between pores 2 and 4 and 6 and 7, and also noted the lack of mandibular canals. Specimens of *A. dispar* also possess pore 1, and three neuromasts apparently corresponding to pores 5 through 7.

Another species, *A. mento*, lacks cephalic sensory pores and has a series of minute neuromasts arranged in a lyre-shaped pattern. Neuromasts ring the orbit and a line of minute neuromasts replaces the preopercular and mandibular canals. The entire system is strikingly like that of the genus *Orestias* (fig. 14) and of the aplocheiloid *Cynolebias* (fig. 13). This character within cyprinodontoids cannot always be distinguished from that in *Cynolebias* (except for the fact that the preorbital area is smaller in the aplocheiloids; yet this character is independent of the preorbital line of neuromasts). A line of preorbital neuromasts is not peculiar to these genera, as it is also found among the fundulines; therefore, the generality of the pattern cannot yet be determined. Consequently, it is assessed as a convergence between members of the genus *Cynolebias* and *Orestias* and a group of Anatolian cyprinodontines.

INTERNAL FERTILIZATION AND VIVIPARITY: Previous workers (e.g., Rosen and Bailey, 1963; Miller, 1979) have assumed that viviparity defines a monophyletic group of cyprinodontiforms, and have therefore focused on describing the similarities and differences of adaptations for viviparity among the families in an effort to determine which viviparous family was more closely related to which other such family. In the present study, this presumption was discarded at the

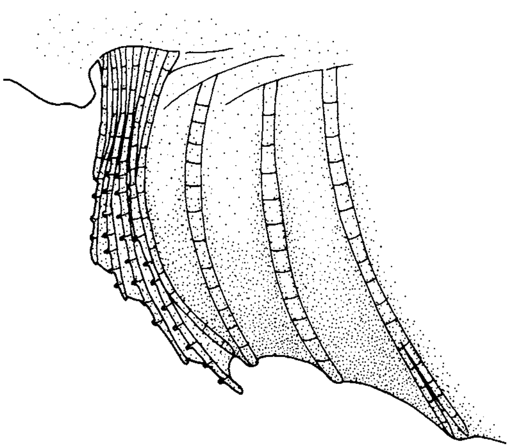

FIG. 63. Diagrammatic representation of first several rays of the anal fin of a male *Cynolebias* (*Cynopoecilus*) *melanotaenia*. External view.

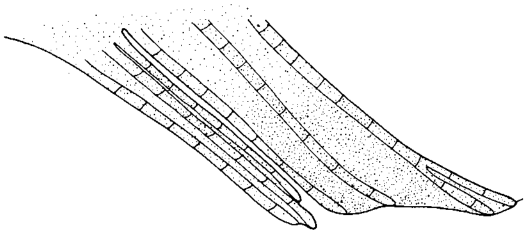

FIG. 64. Diagrammatic representation of first several rays of the anal fin of a male *Cynolebias* (*Campellolebias*) *brucei*. External view.

outset. The simple division of cyprinodontiforms into oviparous and viviparous groups is an artificial one, and grossly oversimplifies the question of cyprinodontiform interrelationships.

Internal Fertilization and Anal Fin Modification: Internal fertilization occurs in groups of atherinomorph fishes with and without an anal fin modified into a gonopodium. Developing embryos have been found in the body cavity of the ricefish *Oryzias* (Amemiya and Murayama, 1931), yet no modifications in the anal fin structure of this genus have been reported.

Among aplocheiloids, a group of Neotropical genera are distinguished by the thickening of the anal rays of the females. All included species are annual, and this has been suggested as an aid to the depositing of eggs in the substrate during fertilization (Weitzman and Wourms, 1967).

The anal fin of aplocheiloids is typically unmodified, except in two species placed here in the genus *Cynolebias*: *melanotaenia* (Regan) and *brucei* (Vaz-Ferreira and Sierra). In *melanotaenia*, the first six anal rays of the male are crowded together (fig. 63) and slightly offset from the rest of the fin. The rays are covered with small contact organs. In *brucei* (fig. 64) the first three anal rays are drawn together to form what is effectively a true gonopodium. Both cases are inferred to represent modifications for internal fertilization, yet both species are oviparous as well as annual.

Females of *brucei* isolated after being in contact with males have laid fertilized eggs (Vaz-Ferreira and Sierra, 1974). Presumably, once the eggs are laid, they develop in a fashion typical of their annual relatives.

One other case of internal fertilization occurs within aplocheiloids in *Rivulus marmoratus*. Populations of this species have been found consisting of self-fertilizing hermaphrodites and possess color patterns indistinguishable from females of the species (Harrington, 1961). This self-fertilization, of course, involves no modification of the anal fin. The fertilized eggs of *marmoratus* are laid as in *C. brucei* and *melanotaenia*, thus there are no known cases of embryo retention among the aplocheiloids.

Among cyprinodontoids, internal fertilization has been demonstrated only among the viviparous families; however, its discovery in an oviparous cyprinodontoid would not be surprising, considering the generality of the condition.

Structure of the gonopodium: Among the viviparous families there are three basic types of anal fin modifications of the male which effect internal fertilization. These are the gonopodia of poeciliids, the tubular gonopodia of *Jenynsia* and *Anableps*, and the muscular internal organ and slightly modified anal fin of the goodeids.

The structure and development of the gonopodium of the poeciliid fishes has been discussed in detail (Rosen and Bailey, 1963; Rosen and Gordon, 1953; Rosen and Kall-

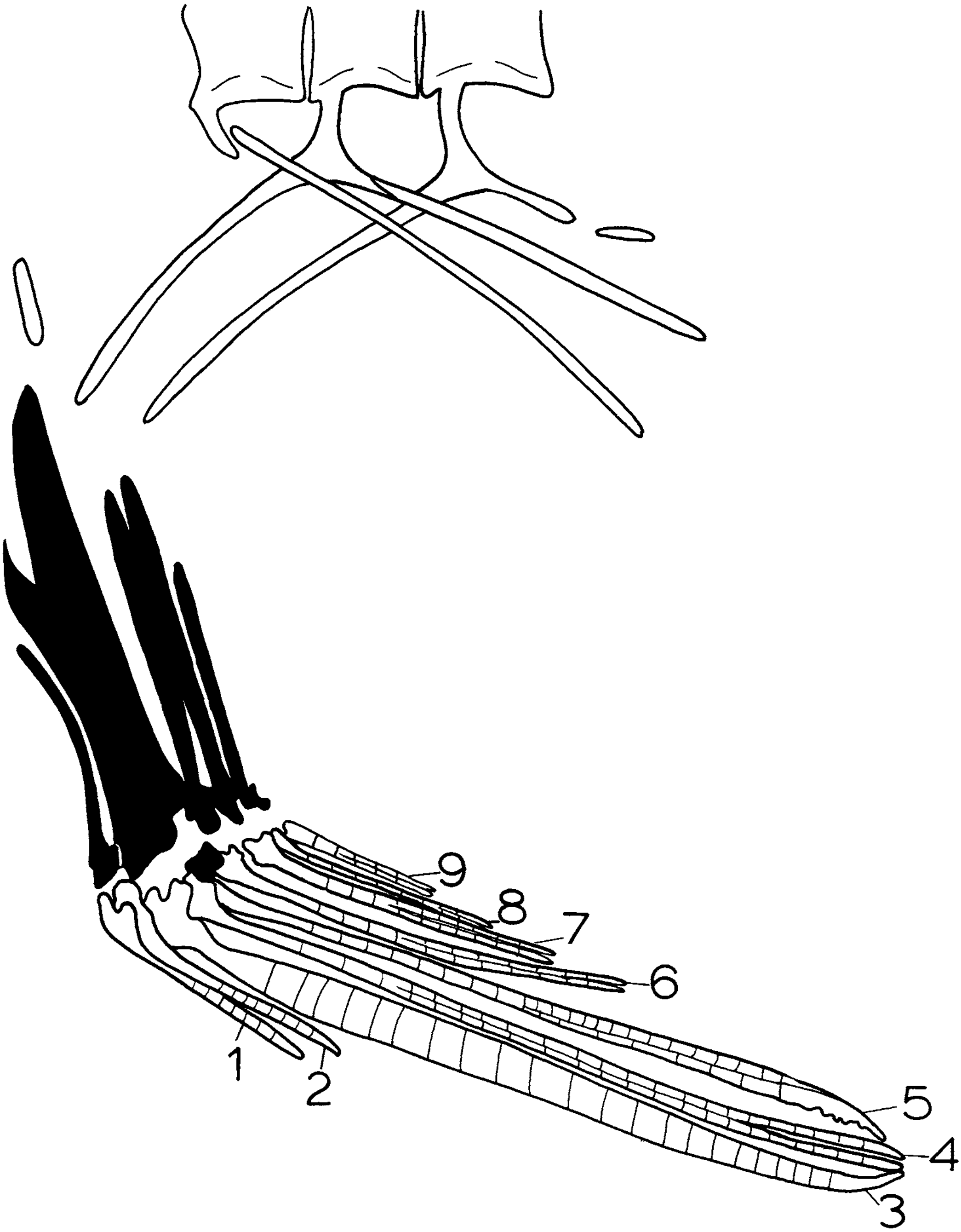

FIG. 65. Diagrammatic representation of gonopodium and gonopodial suspensorium of *Poecilia vivipara*. Anal radials are blackened.

man, 1959). The gonopodia and gonopodial suspensoria vary among taxonomic groups of poeciliid fishes; it is primarily on these structures that such groups are defined.

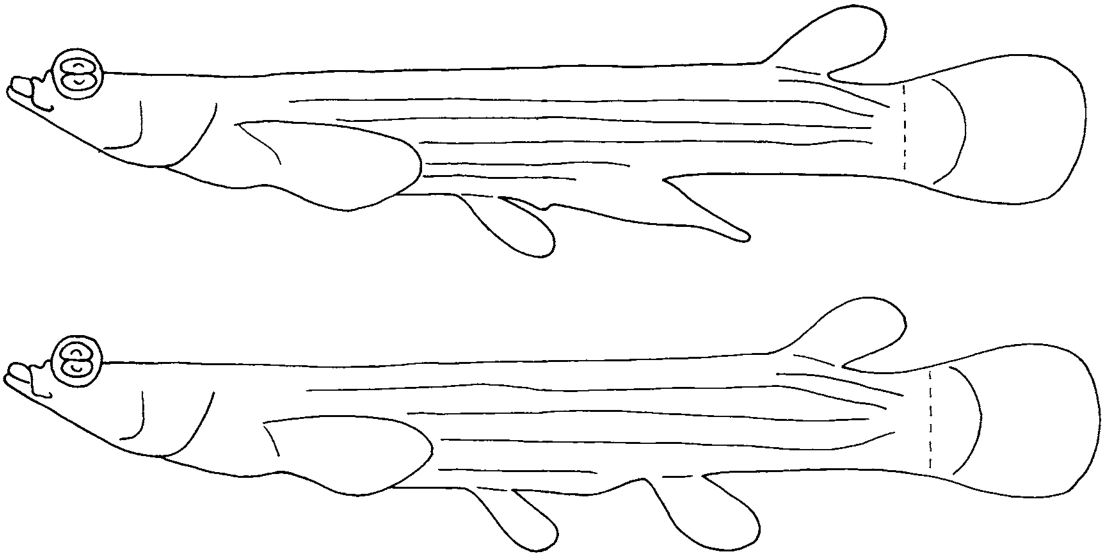

FIG. 66. Sketch of body form and fin position of *Anableps microlepis*, male above, female below. Dotted line approximates base of hypural plate. (After Rosen, 1973b.)

The poeciliid gonopodium (fig. 65) is formed principally from the third, fourth, and fifth anal rays. Transformation from an undifferentiated anal fin begins with a thickening of the third anal ray. In all poeciliids the first three anal rays are unbranched.

There is a rapid growth of rays three through five to form the so-called 3-4-5 complex. Further elaboration and growth occur, resulting in a gonopodium which is often adorned with various spicules, hooks, and spines.

Internal supports are modified within poeciliids to a greater degree than in the other viviparous families. Again, as in *Poecilia vivipara* (fig. 65), the proximal anal radials two through five are elongated. Histolysis of the first hemal arch results in an ossified remnant termed the ligastyle, which migrates anteriorly. In addition, the second, third, and sometimes fourth hemal arches are expanded, the distal tips of which project anteriorly to meet the anteriorly projecting tips of the proximal anal radials.

*Anableps* and *Jenynsia* have a tubular gonopodium formed from enlarged anal fin rays covered anteriorly with a fleshy sheath (fig. 66). In *Anableps*, the sheath is covered with scales; in *Jenynsia* it is bare.

Internally, the structures are similar in that the anal rays are twisted around each other (figs. 67, 68). Similarly, there is an enlargement of the proximal anal radials, as well as an elongation of the hemal spines. Gonopodial development in *Jenynsia* and *Anableps* differs considerably; neither resembles that of the 3-4-5 complex typical of poeciliids, however.

In *Anableps*, the gonopodium is formed from the 12 anal fin rays, counting each ray separately. The first ray is rudimentary, nonetheless it will be referred to as ray 1, contrary to the convention established by Turner (1950).

The first four rays are unbranched. Rays three through six are enlarged and twisted around each other (fig. 67), whereas seven through nine are also enlarged but lie straight. Rays 10 through 12 are drawn forward in the formation of the tubular sheath, but otherwise undergo little differentiation.

The proximal radials are also enlarged, drawn together and angled anteriorly. The first four or five proximal radials are offset

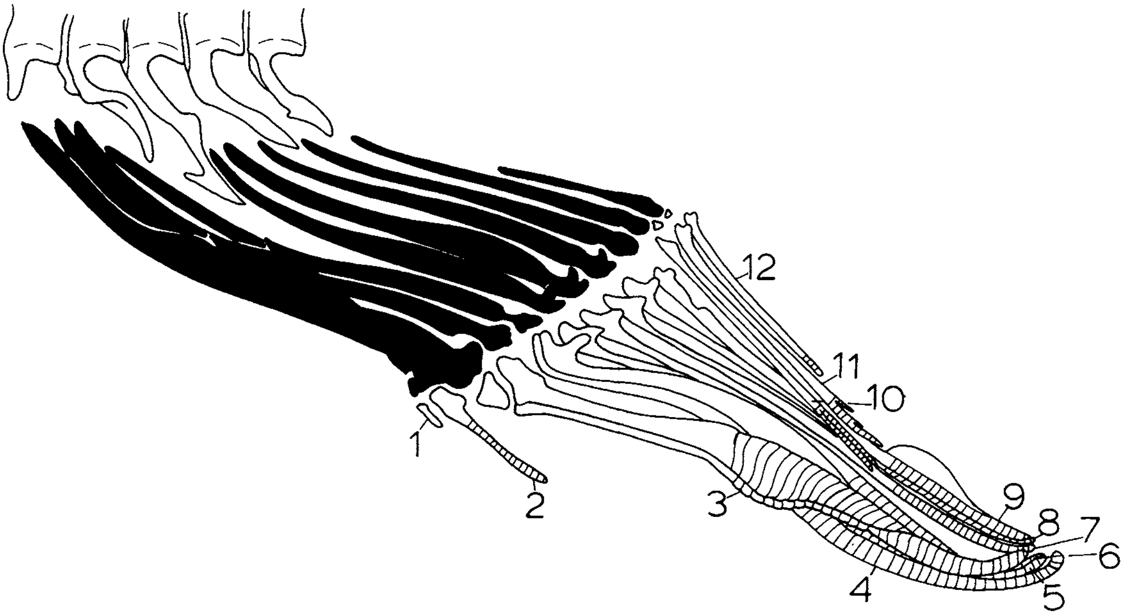

FIG. 67. Diagrammatic representation of gonopodium and associated elements of *Anableps*. Anal radials are blackened. (After Turner, 1950.)

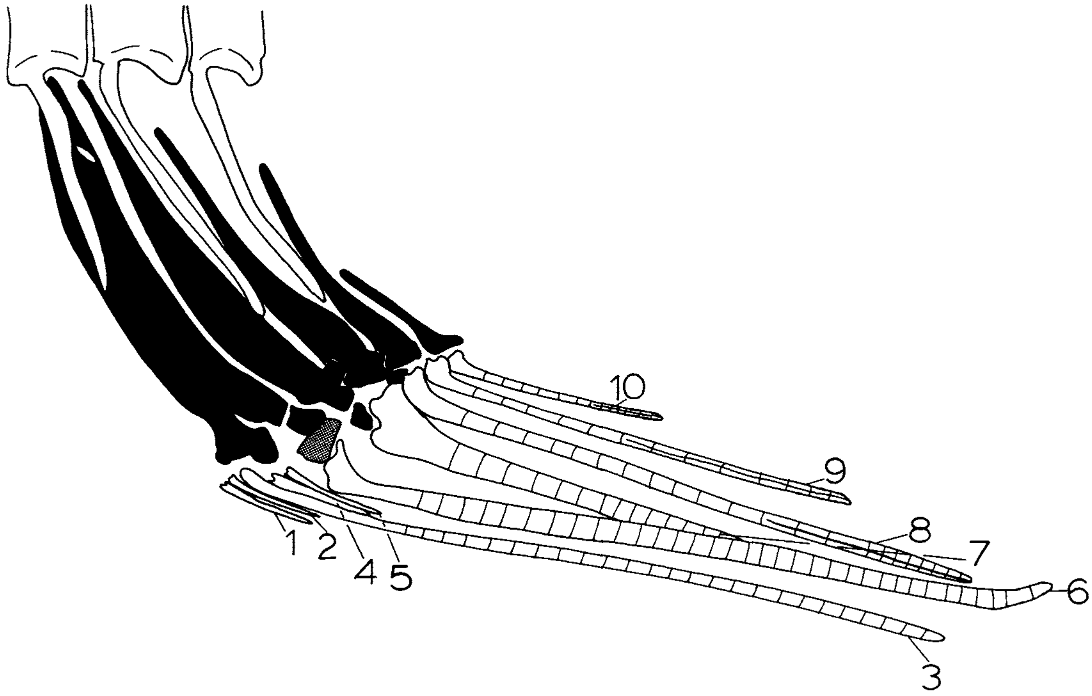

FIG. 68. Diagrammatic representation of gonopodium and associated elements of *Jenynsia lineata*. Sixth middle anal radial is stippled; all other radials are blackened.

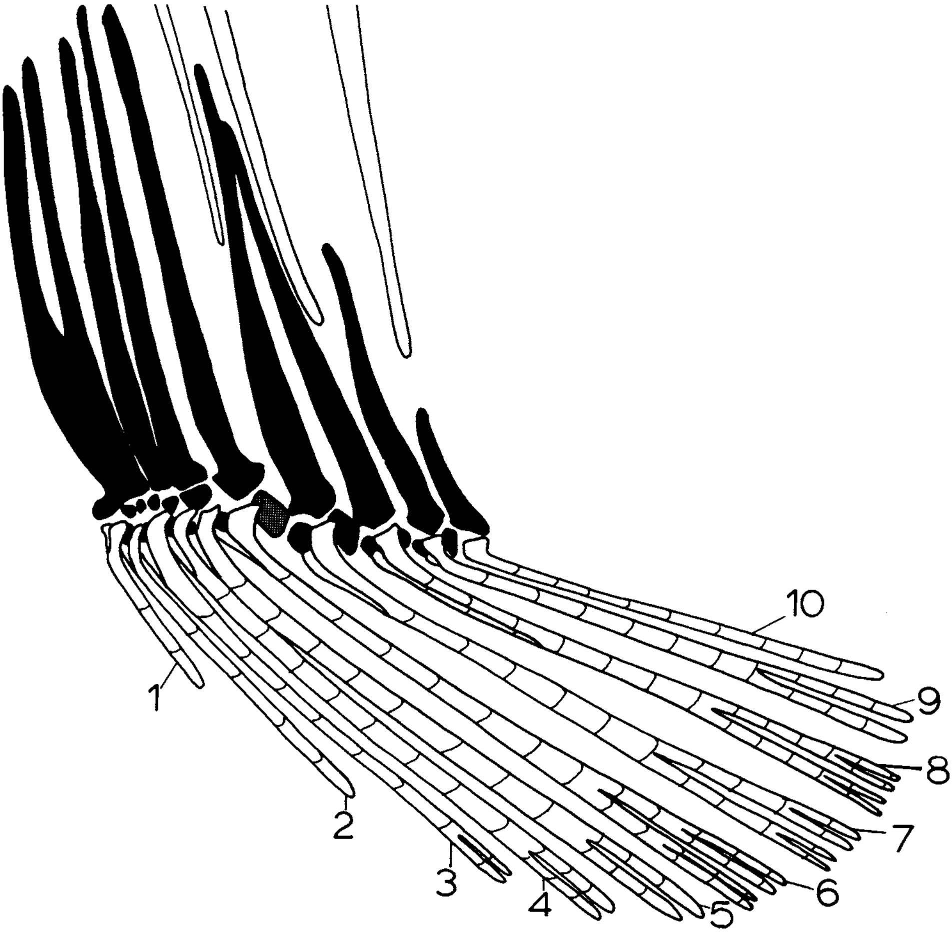

FIG. 69. Diagrammatic representation of the anal fin of a female *Jenynsia lineata*. Sixth middle anal radial is stippled; all other radials are blackened.

to either the left or the right of the midline in sinistral or dextral males, respectively; they extend to just beneath the vertebral column. Typically, there is histolysis of the last several pleural ribs. The hemal spines, especially the first three, extend ventrally and are situated between the proximal radials. At their bases these radials typically have bony flanges which project dorsally. Similarly, the bases of the anal fin rays are greatly enlarged and have similar flanges which overlap on adjacent rays. A full complement of middle and basal radials appears to be present, although Turner (1950) did not illustrate all of these for his specimen.

In *Jenynsia* (fig. 68) the gonopodium is formed from 10 anal rays; however, its development involves primarily reductions of some elements found typically in the female anal fin. Therefore, the anal fin of the female will be described first so that a comparison with the structures within the gonopodium may be made easily.

In an adult female *Jenynsia* (fig. 69) there are 10 anal rays, counting the last two separately. The first two rays are unbranched. The first six rays are crowded together; there is a corresponding crowding and reduction of the first five middle anal radials. The first two proximal radials are fused at their base.

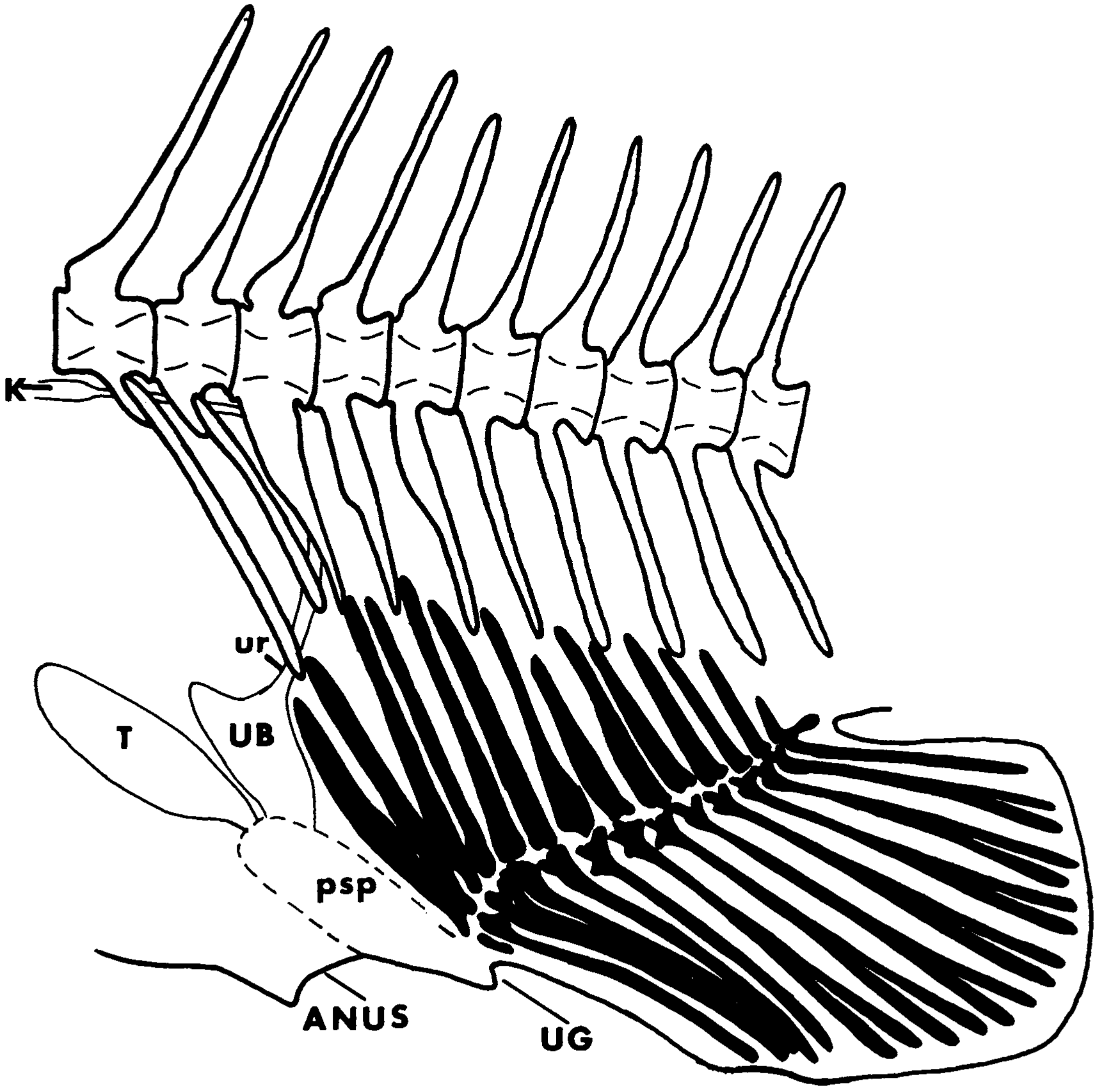

FIG. 70. Diagrammatic representation of the internal structure of the abdominal cavity, anal fin rays and vertebral column of *Characodon lateralis*.

There appears to be no separate proximal radial for the first anal ray; however, it is possible that the radial has become fused to the base of the recognized first radial which has a small bony knob projecting anteriorly. This interpretation is supported by the fact that there are three middle radials present corresponding to the large proximal radial. Five proximal radials all lie anterior to the elongate first hemal spine.

In an adult male *Jenynsia* the sixth middle anal radial is the first unreduced radial as it is in the female (fig. 69), and as in the female, five rays precede and four rays follow this radial. Of the first six rays, all but rays 3 and 6 are extremely reduced. The seventh and eighth rays, as well as 3 and 6, are elongate and thickened; together with the relatively unelaborated segments of the ninth ray, they constitute the principal rays of the gonopo-

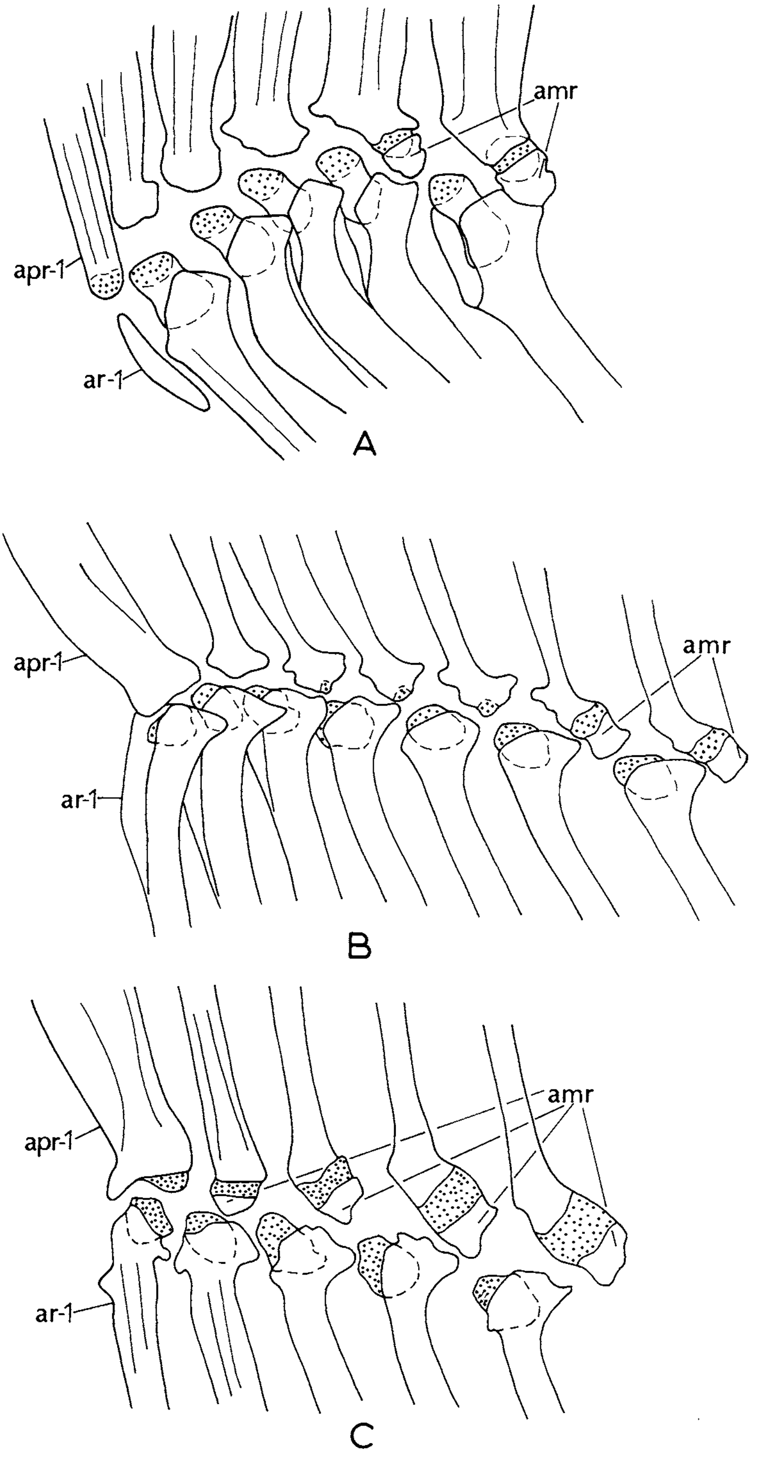

FIG. 71. Anterior rays and supports of the anal fin of a male A. *Characodon lateralis*; B. *Crenichthys baileyi*; C. *Empetrichthys merriami*. Cartilage is stippled.

dium. Ray 6, the thickest and the longest, is hooked at its tip. The proximal radials, especially those of rays 2 through 6, are crowded together more so than in the female. These radials appear to be fused in part, although they have not been observed completely fused. All radials appear to be present, but identification of individual segments is difficult.

In male and female *Jenynsia*, there are bony flanges on the base of the rays and the proximal radials. The proximal radials are offset to the midline in males, corresponding to the laterality of the individual as in *Anableps*; a dextral male is illustrated. A ligastyle has been found in *Jenynsia* males, as in poeciliid males. In addition, the gonopodium of *Jenynsia* is similar to that of *Anableps* and differs from that of the poeciliids in having the proximal radials enlarged and angled forward to the left or right; there are never enlarged hemal arches which project anteriorly to meet the proximal radials of the anal fin which migrates anteriorly in its development within the poeciliids.

The structure of the jenynsiid gonopodium differs from that described by Turner (1950) who stated (p. 352): "most of the rays in the anterior part of the fin undergo absorption . . . ." It agrees more with that of de Gil (1949) who illustrated several variations in the formation of the fin, but in each case indicated that all the fin rays were present.

The anal fin of the goodeid males is relatively unmodified compared with those of the poeciliid, jenynsiid, and anablepid fishes. The structure is not properly termed a gonopodium, as the modifications of the anal fin elements themselves appear to have little to do directly with the transfer of sperm.

Goodeid males, however, are diagnosable on the basis of anal fin structure. The first six or seven fin rays are shortened and unbranched, and offset from the rest of the fin rays (fig. 70). The first anal fin ray is rudimentary, and the middle radials of the first six or seven rays are fused to the base of the proximal radials. Taken together with the presence of trophotaeniae in embryos, these characters were used by Miller and Fitzsimons (1971) to define the Goodeidae.

The rudimentary anal ray is formed to varying degrees among members of the family (Miller and Fitzsimons, 1971). The first four to seven middle anal radials are not present as distinct structures in all goodeids examined (e.g., as in *Characodon lateralis*, fig. 71A). However, among cyprinodontiform fishes, middle anal radials are fused to the proximal radials in the two North American genera suggested as close relatives of the goodeids, *Crenichthys* and *Empetrichthys*. In *Crenichthys baileyi* (fig. 76), the first five middle radials are lacking. In *Empetrichthys merriami* (fig. 71C) the first proximal radial is fused and there is no first or second middle radial; the third middle radial is represented by a minute ossification at the base of the third proximal radial.

The proximal radials corresponding to the shortened anal fin rays are greatly elongate in goodeids (fig. 70). They are not fused together as in the other viviparous families, however. The proximal radials of *Empetrichthys* and *Crenichthys* are slightly elongate; however, they differ little from that of a typical oviparous cyprinodont (fig. 22).

In the ontogeny of anal fin rays, all are formed unbranched and then successively become branched. In both *Oryzias* and *Menidia*, the number of unbranched anal rays is two, as it is in many cyprinodontoids. Among the aplocheiloid fishes which have lost the first proximal anal radial, there are often three unbranched anal rays. The number of unbranched rays varies among cyprinodontiforms from no rays unbranched in an occasional specimen of *Profundulus* (Miller, 1955a) and in members of the genus *Orestias* to all but one unbranched in some fundulines and cyprinodontines. In all poeciliids, as well as the genus *Pantanodon* and at least one nominal species of *Aplocheilichthys*, *A. johnstoni*, there are three unbranched anal rays. In *Anableps* there are four in males and three in females, whereas there are two in both males and females of *Jenynsia*. Among the goodeids, the unbranched anal fin rays typically number more than four.

Considering the ontogeny of anal fin rays, it could be argued that a high number of unbranched rays is primitive, while successive-

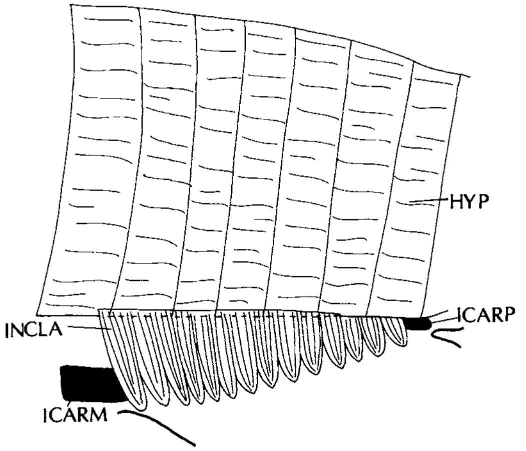

FIG. 72. Diagrammatic representation of the generalized primitive state of the anal fin musculature in cyprinodontiforms.

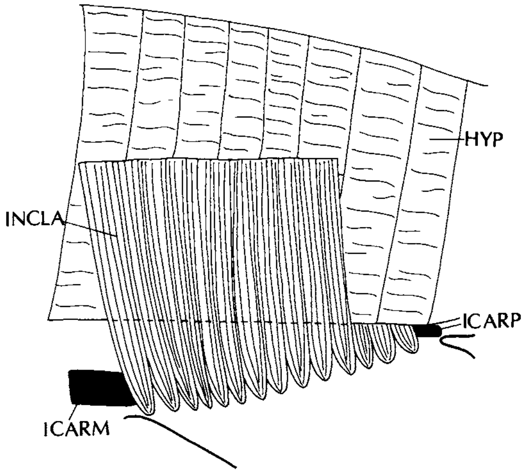

FIG. 73. Diagrammatic representation of the derived anal fin musculature of cyprinodontiforms.

ly lower numbers are derived. Conversely, a certain number of rays could be primitive for a group, and the suppression of branching a derived modification. I accept the latter viewpoint since it is the description of characters in their adult form whose distribution must be analyzed without recourse to presumptions about varying ontogenies. Thus, the increase in unbranched anal fin rays above one or two is hypothesized to be a derived character among cyprinodontiforms.

Anal Fin Musculature: The anal fin musculature of the aplocheiloids which exhibit internal fertilization, *C. melanotaenia* and *C. brucei,* is of the primitive type for cyprinodontiforms (fig. 72). That is, there is a set of external inclinators as well as erectors and depressors corresponding to the individual anal fin rays. One broad band of muscle, the infracarnalis medius runs from the base of the pelvic fins to the first anal radial; a second, the infracarnalis posterior runs from the last anal radial to the distal tip of the last hemal spine (Winterbottom, 1974).

In male poeciliids, the anal inclinators are drawn together into a fan-shaped mass of muscle. In *Anableps* and *Jenynsia,* there are no such fan-shaped masses of muscles. The inclinators are thickened, otherwise the muscles differ little from those of the generalized type.

Nelson (1975) discussed the mechanism of sperm transfer in the goodeids, and illustrated the anal fin muscles. Such muscles in goodeids diverge most from the generalized type in forming a large muscular mass surrounding the vas deferens and urinary tract in a structure which was termed a pseudophallus by Mohsen (1961a). Along with this urogenital organ, is an elaboration of the inclinators of the anal fin. The inclinators, which arise between the hypaxial musculature and insert on the bases of the anal fin rays distal to the insertion of the erectors and depressors (Winterbottom, 1974), arise just below the division of the epaxial and hypaxial musculature (fig. 73). Such elaborate inclinators, however, are not restricted to the goodeids. They are found also in a group defined above on the basis of skull and jaw specializations, viz., *Empetrichthys, Crenichthys, Cubanichthys, Chriopeoides, Orestias,* and the cyprinodontines.

SPERM TRANSFER: Sperm transfer occurs in poeciliids when the gonopodium is swung forward and folds over to one side or the other to form a groove. Sperm pass down the groove in unencapsulated bundles termed spermatozeugmata and are transferred to the female by application of the gonopodial tip to, or within, the genital pore.

In some poeciliids the pelvic fins are also modified in the males. Clark and Kamrin (1951) report that in a number of poeciliids tested, the pelvic fin of one side is swung forward together with the gonopodium. They speculated that the pelvics in such species contribute to the formation of the sperm groove.

In the poeciliids, procatopines, *Pantanodon* and *Fluviphylax,* pelvic fins are set far forward and are often under the pectoral fin bases (e.g., in the poeciliid *Heterandria bimaculata,* fig. 52 and in the procatopine *Procatopus glaucicaudus,* fig. 53). The thoracic or subthoracic position of the pelvic fins in these groups results from an ontogenetic forward migration during sexual differentiation. This fact has been well known within the poeciliids for some time (Clark and Kamrin, 1951; Rosen and Kallman, 1959); however, the phenomenon in the procatopines and other genera is little known. Trewavas (1974) reported data for several species of *Procatopus* from West Cameroon to support the fact that the pelvic fins indeed migrate forward in ontogeny. The extent of this phenomenon among procatopines is not known and could properly be explored with laboratory developmental series of representatives of all procatopine genera as well as *Fluviphylax* and *Pantanodon.*

Within *Anableps* and *Jenynsia* the tubular gonopodium is associated with a distinctive mode of sperm transfer. In both genera, all the rays of the anal fin are brought close together and surrounded by a fleshy tube (fig. 66). The sperm duct enters the tube at the base of the first anal ray and follows the ventral edge of the tube to its tip. Sperm do not travel down the tube in sperm bundles, but individually. Grier, Burns and Flores (MS) report that partial sperm bundles are formed in *Anableps dowi,* the presumed primitive species of the genus (Miller, 1979) but break down before they enter the sperm duct; only free spermatozoa were observed in both the efferent and main testes ducts of *A. anableps* and *Jenynsia lineata.* The abdominal pelvics of *Jenynsia* and *Anableps* are inferred to have no function in sperm transfer.

Since Garman (1895) described the presence of sexual lefts and rights in *Anableps* and *Jenynsia* the phenomenon of dextral males pairing with sinistral females (and vice versa) has been reported tentatively in the literature (e.g., Rosen and Bailey, 1963) although its occurrence is still doubtful (Miller, 1979). In theory, there are two kinds of males, sinistral and dextral and corresponding types of females. A dextral male supposedly has a gonopodium which is offset to the right; therefore, he can only copulate with a sinistral female. The sidedness of a female is determined by the placement of one or two scales over one side of the urogenital opening; hence a scale covering the left side of the opening defines a female as dextral. Individuals, although they may easily have their laterality determined, have not been observed to be either exclusively dextral or sinistral in their mating (Miller, 1979). Thus, the significance of the anatomical modifications related to sidedness remain speculative.

Although laterality is not evident among young males of *Anableps* examined, adult males could easily be classified as left or right. Females' sidedness is also generally easy to determine; however, some large adult female *Anableps* seem to be neither left nor right.

In the oviparous *Oxyzygonectes,* a hypothesized close relative of *Jenynsia* and *Anableps,* males have a distinct anal papilla which in preserved specimens has been observed to be offset to the left or to the right. The significance of this character is equivocal since it may simply be an artifact of preservation. Females offer no clue since they possess a fleshy pouch surrounding the genital opening. Both male and female *Oxyzygonectes,* however, have scales around the anterior region of the anal fin much like the pocket of scales surrounding the anus and first several anal fin ray bases considered to be a diagnostic character of the procatopines (Clausen, 1967). This pocket of scales apparently is a derived character of the larger group including the poeciliids, *Jenynsia, Anableps,* the procatopines, *Fluviphylax* and *Pantanodon* as well as *Oxyzygonectes.* If so, these scales have been modified or reduced in the viviparous forms.

Sperm bundles are formed in the goodeids (Grier, Fitzsimons and Linton, 1978), although the precise mechanism of sperm transfer is still unknown. Mohsen (1961a, 1961b) described a muscular organ surrounding the vas deferens and urinary canal and believed that sperm bundles were ejected during copulation by a contraction of the organ. Nelson (1975) reported that during a copulation attempt, the male clasps the female: the anterior portion of the anal fin formed by the shortened rays is wrapped around the genital opening of the female while the notch in the fin is placed near the anterior margin of the anal fin of the female. Thus, the urogenital organ of the male comes very close to the female's urogenital opening.

True spermatophores, that is, encapsulated sperm bundles, occur only in the adrianichthyoid *Horaichthys* (Kulkarni, 1940). Sperm bundles, however, occur among several teleost groups including the cyprinodontiforms just mentioned and the exocoetoid *Dermogenys* whose sperm bundles are indistinguishable from those of the poeciliids (Grier, Burns and Flores, MS). Free spermatogonia, like oviparity, must be considered a primitive character. However, the occurrence of spermatozeugmata with viviparity among different relatively unrelated groups suggests that spermatozeugmata have arisen independently along with viviparity.

Fertilization and Development: The distribution of characteristics related to egg retention and maternal contribution to development precludes the ready division of members of the four so-called viviparous families into oviparous, viviparous and ovoviviparous groups.

Among the poeciliids, one genus and species, *Tomeurus gracilis*, is oviparous and just facultatively viviparous (Rosen and Bailey, 1963). Fertilization takes place as in all other poeciliids, within the follicle; however, the developing embryo is quickly released from the ovary into the oviduct and then passed to the outside for the remainder of the developmental period. The egg of *Tomeurus* has a thick chorion with adhesive filaments like that in oviparous cyprinodontiforms. Among other poeciliids, the egg retains an extremely reduced chorion (Zahnd and Porte, 1962; Flegler, 1977). Also among the poeciliids are found some of the smallest vertebrate eggs (Scrimshaw, 1946).

Ovoviviparity may be identified in certain groups of poeciliids, for example *Brachyrhaphis episcopi* (Turner, 1938). The yolk sac is relatively large, and although development is internal, nutritional support is derived primarily from the yolk.

Development of fertilized eggs in the rest of the true viviparous poeciliids is of two major types (Turner, 1939). In *Heterandria formosa,* for example, a so-called pseudochorion and pseudoamnion are formed by the folding around the embryo of extraembryonic somatopleure in the pericardial region. The outer membrane thus formed is termed the pseudochorion; it is highly vascularized, whereas the inner pseudoamnion is nonvascular. The pseudochorion is used as an organ for respiration and nutrition throughout development. In species of *Poeciliopsis,* which also have small yolk reserves, the lateral region of the somatopleure is poorly developed. The ventral region becomes highly vascularized and invades the region between villi formed in the follicular membrane; together they form what is termed a follicular pseudoplacenta. Thus, the embryos of *Heterandria formosa* and *Poeciliopsis* and related species derive the greater part of their nutrition from maternal tissues rather than from stored yolk. Poeciliids also exhibit the phenomenon of superfetation, that is, the overlapping of developing broods in the ovary (Scrimshaw, 1944).

Anablepid, jenynsiid, and goodeid fishes exhibit more elaborate adaptations for viviparity.

In *Anableps,* both fertilization and development are intrafollicular as in poeciliids. In addition, a follicular-pseudoplacenta more elaborate than that of the poeciliids is also developed. The ventral portion of the somatopleure expands to form highly vascularized projections; the surrounding follicle is covered with vascular villi. In *Anableps dowi,* the species presumed to be most primitive, the large intestine expands and nearly fills this sac. Follicular fluid is absorbed by the embryo across intestinal villi. At birth, the follicle ruptures and the expanded belly sac eventually undergoes shortening.

In jenynsiids, although fertilization is intrafollicular the embryo is evacuated from the follicle and development takes place within the ovary. Development is viviparous rather than ovoviviparous since the yolk supply is consumed at an early stage, and nutrition is derived mainly from maternal fluids. Respiration occurs across an expanded ventral somatopleural sac as in the anablepids. Maternal fluids enter the developing embryo through its mouth or through the opercular openings (Turner, 1940b). Flaps grow out from the wall of the ovary and invade the opercular region and an intimate connection between embryo and mother is provided as the flaps of tissue invade the pharyngeal and buccal cavities.

In goodeids, as in jenynsiids, the eggs are fertilized in the follicles and then released into the ovarian cavity for development. Goodeids are characterized by the possession of trophotaeniae (Turner, 1937), elaborate outgrowths in the perianal region, the epithelium of which possesses villi and is indistinguishable from intestinal epithelium (Wourms and Cohen, 1975). Their function as absorbers of nutritive ovarian fluids is inferred from their structure.

Morphology of the trophotaeniae and of the ovary served as the principal character for the last general revision of the Goodeidae by Hubbs and Turner. However, more recently, Miller and Fitzsimons (1971) have reviewed the classification and concluded that the great degree of variability among these structures makes them of little importance in phylogenetic studies. Miller and Fitzsimons did not propose a reclassification.

Goodeid ovaries (median organs formed by fusion of right and left anlagen) fall into one of two main types (Hubbs and Turner, 1939): (1) an ovarian septum and outer wall composed of ovigerous tissues, the inner septum is often folded down the middle of the joint ovarian cavity; and (2) an ovarian septum and outer wall which is devoid of ovigerous tissue, the structure of which is as two folded masses, one in each section of the ovary. The first of these is apparently the primitive state of the fused ovaries, and the second the more derived state with ovigerous tissue excluded from the walls and septum and confined to the middle of the ovarian cavities. In one genus and species, *Characodon lateralis,* there is an intermediate type of ovary which has ovigerous tissue both in a short section of the septum and in weakly formed tissue extensions into each of the ovarian cavities. This so-called intermediate condition, however, may be more accurately assessed as more closely related to the derived type 2; that is, it forms a transition between the distinctly primitive and derived types.

Trophotaeniae occur in three types: rosette or ribbon-like, and when ribbon-like, sheathed or unsheathed. In a sheathed process the external epithelium is separated from the internal connective tissue by a wide space, thus giving the external epithelium the appearance of a thin external covering (Wourms and Cohen, 1975).

Mendoza (1965) studied the ontogeny of trophotaeniae and found that all are first formed as rosette perianal outgrowths; these are then elongated in those goodeids which have ribbon-shaped trophotaeniae. Thus, based on ontogenetic information, the rosette type of trophotaeniae is primitive, whereas the ribbon-like processes are derived. The significance of a sheathed versus unsheathed process is questionable since the rosette is histologically identical to the sheathed process (Wourms and Cohen, 1975).

Hubbs and Turner (1939) classified the goodeids in four subfamilies: the Ataeniobinae consisting of one genus and species, *Ataeniobius toweri* which lacks trophotaeniae altogether and possesses the primitive type of fused ovary; the Goodeinae which possesses the primitive rosette type of trophotaeniae and the primitive type of fused ovary; the Characodontinae, consisting solely of *Characodon lateralis,* which has a type of ovary distinctly intermediate between the primitive and derived type, and sheathed ribbon-like trophotaeniae; and the Girardinichthyinae which has the derived type of ovary and sheathed ribbon-like trophotaeniae.

If, as suggested, *Characodon* and the Girardinichthyinae can be considered sister groups on the basis of their sharing derived trophotaeniae and ovaries, then the Goodeinae and possibly *Ataeniobius* represent an intermediate assemblage between the common ancestor of the goodeids and these two more derived subfamilies. Thus, the Goodeinae is a paraphyletic subfamily as it has no defining characteristics. The status of *Ataeniobius* is still problematic since its lack of trophotaeniae may be assessed as a loss character if, on the basis of other characteristics, it is assessed as more closely related to the more derived goodeids. The problem with goodeid classification is that it is currently based only on transition series of two characters and does not take into account the apparent osteological and internal and external morphological differences among genera.

SUMMARY OF VIVIPARITY: The peculiarity of cyprinodontiform reproduction in general is a long developmental period associated with an early breeding habit.

Viviparity occurs in teleosts outside cyprinodontiforms in the Hemirhamphidae and Oryziatidae in atherinomorphs, and for example, zoarcids, scorpaenoids, and ophidioids in the percomorphs. In addition, trophotaeniae are not unique to the goodeids; they occur in nearly the same form and therefore have the same inferred function in embryos of the zoarcids and ophidioids (Wourms and Cohen, 1975; Cohen and Wourms, 1976). The similarity of the gonopodia of *Tomeurus* and *Horaichthys* has long been recognized. However, even if it is allowed that each of these characteristics when it appears in cyprinodontiforms is possibly a uniquely derived character, this possibility may only be evaluated with the use of data from other systems. For example, intrafollicular gestation in poeciliids and *Anableps,* if evaluated as a derived character uniting them into a monophyletic group, makes the family Poeciliidae as currently constituted a paraphyletic group. That is, the complex gonopodia and derived pelvic fins of poeciliids would be judged as independently derived in two groups, once in the poeciliids with intrafollicular gestation and once in all other poeciliids.

Furthermore, the tubular gonopodia formed internally by enlarged and twisted anal rays with laterality determined internally by offset proximal anal radials would have to be considered independently derived in *Anableps* and *Jenynsia.* Neither of these decisions is warranted by the information currently known about adaptations for viviparity, including anal and pelvic fin structures. Therefore, *Anableps* and *Jenynsia* are considered to be sister genera; this decision is supported by the above argument and characters from other systems as discussed.

Similarly, the development of trophotaeniae in both the goodeids and the ophidioids-zoarcids does not support the close relationship of these three groups. Taken independently without knowledge of other characters, trophotaeniae in these three viviparous groups would indeed suggest their close relationship. However, it is only after an assessment of all apparently derived structures that a hypothesis of convergent characters such as the trophotaeniae may be made.

Thus, hypotheses of convergences concerning internal fertilization and viviparity are the following:

1. Internal fertilization occurs independently among the cyprinodontiforms at least five times; in *Rivulus* and *Cynolebias* among the aplocheiloids, and in poeciliids, goodeids, and in *Jenynsia-Anableps* among the cyprinodontoids.
2. Gonopodia occur independently three times; in *Cynolebias brucei* among aplocheiloids and, in poeciliids and in *Jenynsia-Anableps* among the cyprinodontoids.
3. Intrafollicular gestation occurs independently in a group of poeciliids and in *Anableps.*
4. Spermatozeugmata, which occur in all viviparous cyprinodontiforms except *Jenynsia* and outside the cyprinodontiforms, are considered to be independently derived in poeciliids, *Anableps* and goodeids.

These assessed convergences are supported by the following conclusions:

1. The poeciliid gonopodium and gonopodial suspensorium as described herein is a unique complex of characters defining this group.
2. The gonopodia of *Anableps* and *Jenynsia* represent a unique form among teleosts and support the sister group relationship of these two genera.
3. The goodeid manner of internal fertilization with its associated modifications of the anal fin and presence of a copulatory organ as well as a derived ovary and presence of trophotaeniae defined this family as a monophyletic group. Other modifications-support the relationship of goodeids to two North American genera, *Empetrichthys* and *Crenichthys*, and then to a larger group of oviparous cyprinodontoids.

## CLADISTIC SUMMARY OF THE CYPRINODONTOIDS

*Profundulus* (of northern Central America and southern Mexico, fig. 74) is hypothesized to be the most primitive cyprinodontoid genus.

Five species are currently recognized in two subgenera (Miller, 1955a): subgenus *Profundulus* Hubbs with two species, *punctatus* (Günther) and *guatemalensis* (Günther); and *Tlaloc* Alvarez and Carranza with three species, *labialis* (Günther), *candalarius* Hubbs and *hildebrandi* Miller. The genus is defined by a high number of gill rakers on the first arch. The number ranges from 14 to 23 (modally 16), whereas there are four to 14, typically fewer than 12, in *Fundulus* (Miller, 1955a), as well as other fundulines, and a majority of the cyprinodontoids. In the aplocheiloids, the highest number observed is 21 in *Nothobranchius microlepis*. The number of gill rakers is increased in some cyprinodontoids, for example, in *Lamprichthys* and *Pantanodon*. However, the high number in *Profundulus* is considered to be a unique increase and therefore a derived character of the genus. An additional autapomorphy of *Profundulus* is the relatively large autopterotic fossa.

GROUP D: Hypothesized to be monophyletic because its members share the following derived characters: premaxillary ascending processes narrow or absent in adults, while at least weakly formed in embryos or juveniles; rostral cartilage greatly reduced or absent; inner arms of the maxillaries do not abut the rostral cartilage, yet remain attached to it, when present, by connective tissue; and the lateral ethmoid having a greatly reduced facet for articulation of the autopalatine.

FUNDULINES: The term as used throughout this study refers to species of the following nominal genera: *Fundulus* Lacépède, with four included subgenera *Zygonectes* Agassiz, *Xenisma* Jordan, *Plancterus* Garman, and *Fundulus*; *Lucania* Girard, *Adinia* Girard, and *Leptolucania* Myers. The last two genera are monotypic, *Lucania* comprises three species, whereas the genus *Fundulus*, the largest of this group, comprises from 30 to 35 species (Miller, 1955b; Lazara, 1979).

They are hypothesized to form a monophyletic group on the basis of the following derived characteristics of the jaw and skull: inner arms of the maxillaries directed anteriorly and often with pronounced hooks; and snout pointed and drawn anteriorly with the autopalatine projecting anteriorly and not articulating with the lateral ethmoid.

Relationships of the recognized genera as described below are summarized in the cladogram of figure 75; their distribution is given in figure 76.

Two species, *Fundulus kansae* and *zebrinus*, currently placed in the subgenus *Plancterus* are distinguished from other fundulines by having a posttemporal with an ossified, rather than ligamentous, ventral limb. This character is primitive for cyprinodontiforms and may be used to separate *Plancterus* from other fundulines. The two nominal species are regarded as probable conspecifics (Miller, 1955b). The genus *Plancterus* may also be distinguished by a derived character shared by the two species; that is, a rather long and convoluted intestine (Garman, 1895).

Nominal species of the genera *Fundulus*

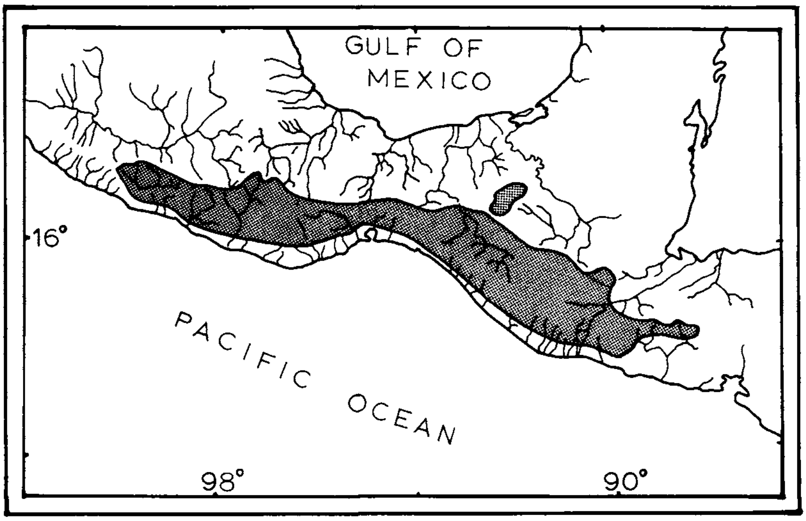

FIG. 74. Distributional limits of *Profundulus*. (After Miller, 1955a.)

(excluding *zebrinus* and *kansae*), *Lucania*, *Leptolucania*, and *Adinia* are linked by the absence of a ventral limb on the posttemporal.

In the most recent review of *Fundulus*, Miller (1955b) listed 26 species in what he called an approximate phylogenetic sequence, although he did not elaborate on the significance of the sequence; he therefore did not recognize the subgeneric divisions of *Fundulus*.

Farris (1968) performed a phylogenetic analysis of the species of *Fundulus* and *Profundulus* and concluded that *Fundulus* was a monophyletic genus comprising the following monophyletic subgenera: *Plancterus*,

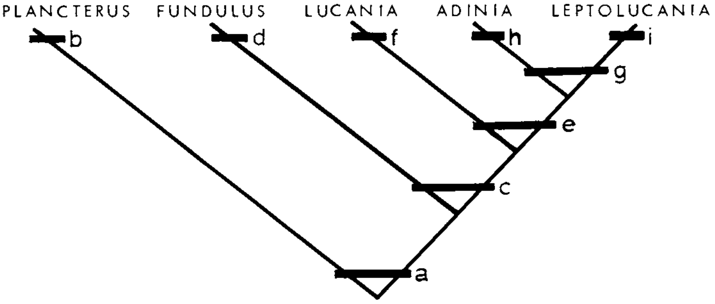

FIG. 75. Cladogram of relationships of the fundulines. Node A: inner arms of the maxillaries directed anteriorly, often with pronounced hooks; snout pointed and drawn anteriorly with the autopalatine projecting anteriorly and not articulating with the lateral ethmoids; Node B: convoluted intestine; Node C: Posttemporal lacks an ossified lower limb; Node D: expanded articular process of the second pharyngobranchial; Node E: epipleural ribs meet the parapophyses of the abdominal ribs at their tips; reduction of the supraorbital pores; Node F: Block of cartilage between the interarcual cartilage and articulation point of the second pharyngobranchial; Node G: No supraoccipital processes; Node H: Quadrangular body form, first pleural rib arises on parapophysis of first vertebra; Node I: three branchiostegal rays, first postcleithrum absent, large black ocellus at midbody and on the caudal peduncle.

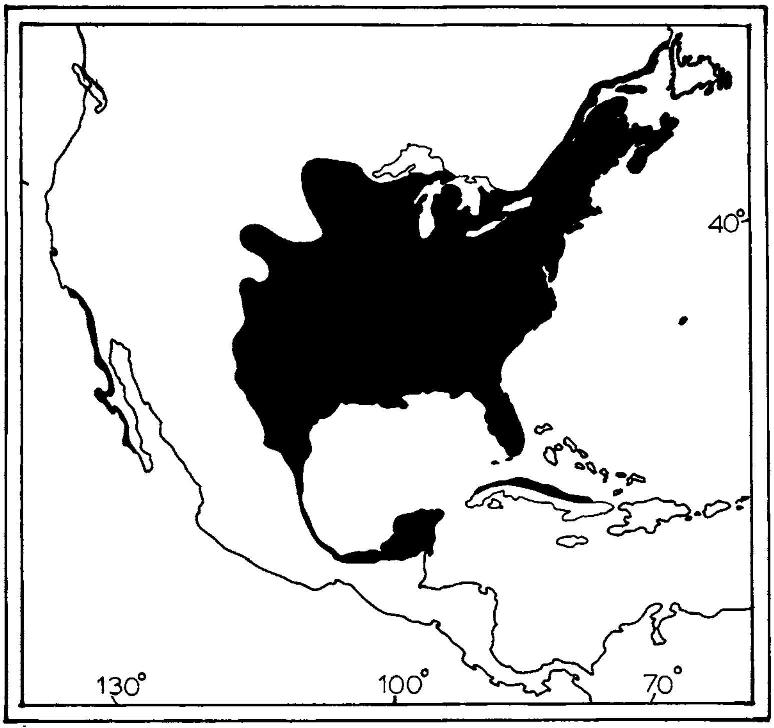

FIG. 76. Distributional limits of the fundulines.

*Xenisma, Zygonectes,* and *Fundulus.* Unique defining characters of the genus and subgenera were not enumerated.

Brown (1957) divided the species of *Fundulus* into the subgenera *Fundulus, Fontinus, Plancterus,* and *Zygonectes* without giving defining characters of each.

With *Plancterus* removed from the genus, *Fundulus* can be defined in having a broad articular surface on the second pharyngobranchial (fig. 46A).

The interrelationships of the species of the subgenera *Xenisma, Zygonectes,* and *Fundulus* have yet to be formally investigated. Wiley and Hall (1975) and Wiley (1977) have presented the only such revision of a group of *Fundulus* species, the *nottii*-complex and three other species all of which would be included in but not totally comprise the subgenus *Zygonectes.* As such, the interrelationships of species and of the subgenera as well as the limits of both categories remain to be determined. However, since the genus is considered to be monophyletic without *Plancterus,* the subgenera *Xenisma* and *Zygonectes* for convenience are treated as synonyms of *Fundulus* in this study.

The remaining funduline genera (*Lucania, Adinia,* and *Leptolucania*) lack the broad articular process of the second pharyngobranchial of *Fundulus,* but are defined by having epipleural ribs attaching directly to parapophyses rather than to pleural ribs. In other cyprinodontiforms the epipleural ribs attach ventrally along the proximal extent of the pleural ribs rather than being in contact with the parapophyses (e.g., in *Aphyosemion occidentale,* fig. 26).

A reduction in the number of supraorbital pores might be an additional derived character of the three genera; however, the difficulty of postulating transition series within the system has been noted already.

There is evidence that each of the three

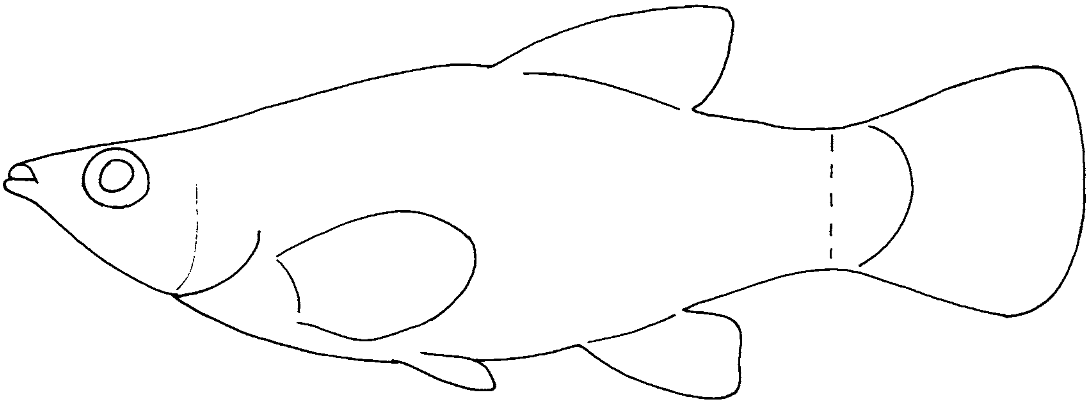

FIG. 77. Sketch of body form and fin position of *Adinia xenica*, male. Dotted line approximates base of hypural plate. (After Rosen, 1973b.)

genera is monophyletic. *Lucania* possesses an apparently unique modification of the dorsal gill arches (fig. 46B). There is a small block of cartilage between the interarcual cartilage and the articulation point of the second pharyngobranchial. No such independent cartilage has been found in other cyprinodontiforms, yet it is present in the species of *Lucania* examined.

The genus *Adinia* is readily separated from the other funduline genera by its laterally compressed, deep-bodied form (fig. 77), described as diamond-shaped or quadrangular. In addition, *Adinia* is unique among cyprinodontiforms in having the first pleural rib arising on the parapophysis of the first vertebra rather than the second.

*Adinia* and *Leptolucania* lack epiotic and supraoccipital processes found among all fundulines and generally among cyprinodontiforms. This condition is considered secondarily derived within these two genera.

*Leptolucania ommata* is a diminutive funduline rarely reaching over 20 mm. standard length. It is unique among fundulines and apparently all cyprinodontiforms in possessing just three branchiostegal rays. These rays number from four to six among other cyprinodontiforms. *Leptolucania* alone among fundulines also lacks the first postcleithrum. The pattern of coloration is also unique. There is a large black ocellus on the caudal peduncle and another at midbody.

The retention of five generic categories comprising the fundulines is deemed appropriate since although *Fundulus* is considered to be monophyletic, all its species have not been examined. It is possible a more parsimonious interpretation would place some species of *Fundulus* as more closely related to *Lucania*, *Leptolucania* or *Adinia*; therefore, a synonymy of all genera now would obscure interrelationships.

CLADISTIC SUMMARY OF FUNDULINES: Fundulines share several derived characters of the jaw and skull: inner arms of the maxillaries are directed anteriorly and often have pronounced hooks, the snout is pointed and drawn anteriorly, while the autopalatine does not articulate with the lateral ethmoid.

*Plancterus* is defined by its long and convoluted intestine.

The four remaining funduline genera, *Fundulus*, *Lucania*, *Adinia*, and *Leptolucania*, are defined as a monophyletic group by their sharing a posttemporal with a ligamentous rather than ossified ventral limb.

*Fundulus* is defined by an expanded articular surface of the second pharyngobranchial. The subgenera *Xenisma* and *Zygonectes* are treated as synonyms of *Fundulus*.

*Lucania*, *Adinia*, and *Leptolucania* are defined as a monophyletic group by having epipleural ribs attaching directly to parapophyses rather than to pleural ribs.

*Lucania* is defined by a small block of car-

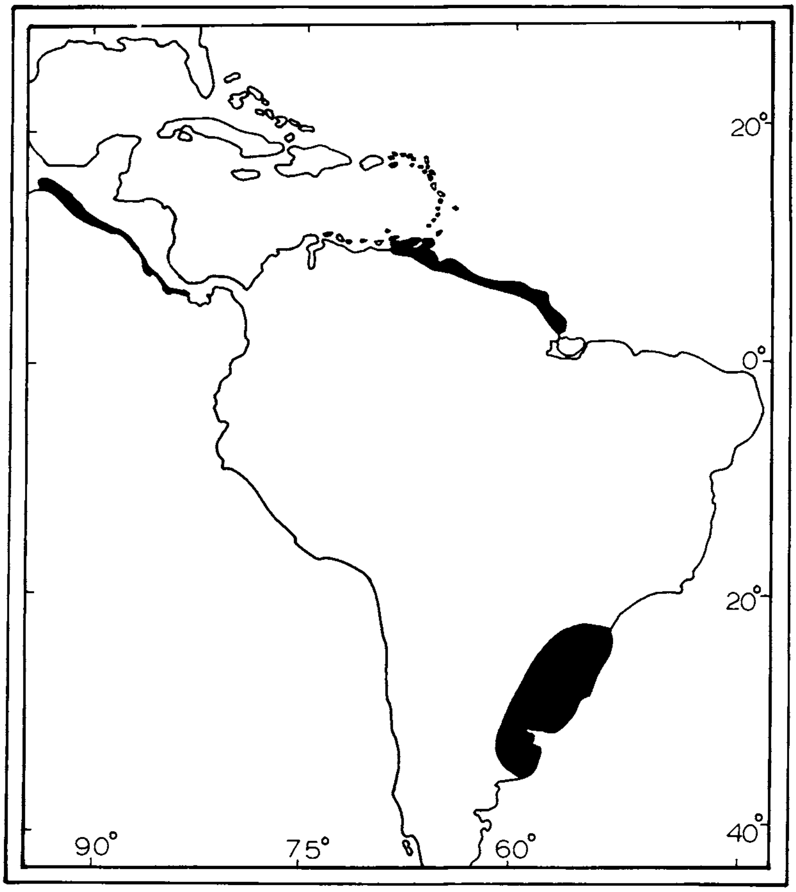

FIG. 78. Distributional limits of *Jenynsia*, *Anableps*, and *Oxyzygonectes*.

tilage between the interarcual cartilage and articulation point of the second pharyngobranchial.

*Adinia* has a unique quadrangular body form as well as the first pleural rib arising on the parapophysis of the first rather than the second vertebra.

*Adinia* and *Leptolucania* lack epiotic and supraoccipital processes.

*Leptolucania* has just three branchiostegal rays, and lacks the first postcleithrum, and has a derived color pattern characterized by a large black ocellus on the caudal peduncle and another at midbody.

GROUP E: Two derived characters define Group E: (1) maxilla with a straight proximal arm, rather than the overtly twisted arm as in aplocheiloids, *Profundulus* and the fundulines, and (2) an enlarged dorsal process of the maxilla directed over the premaxillary ascending process.

*Valencia*: Unique among cyprinodontiforms in having greatly expanded dorsal processes of the maxillaries. The posttemporal also has a ligamentous ventral limb.

GROUP F: Members of Group F share three derived features: (1) the ascending processes of the premaxillaries are short and narrow; (2) the dorsal processes of the maxillaries are rounded or greatly reduced; and (3) the nasals are expanded medially in nearly all members.

GROUP H: The members of Group H share the following derived characters: maxilla

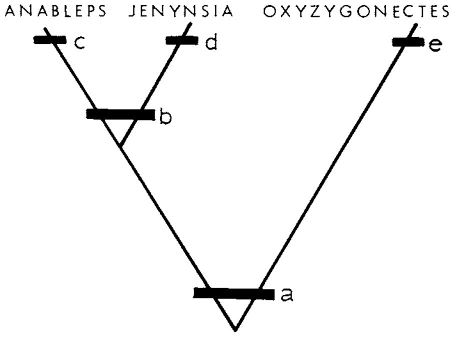

FIG. 79. Cladogram of relationships of *Jenynsia, Anableps,* and *Oxyzygonectes.* Node A: enlarged supraoccipital and epiotic processes; outer and inner teeth with lateral cusps in at least juveniles and embryos; sexual laterality; Node B: thickened and elongated anal rays in male, twisted around each other, covered by a fleshy tube; tubular sperm duct; gonopodium offset either to the left or the right; proximal anal radials enlarged, nearly reaching vertebral column and offset to the left or the right; derived pigmentation pattern (see text); Node C: eyes divided horizontally; supraorbital processes of frontals expanded; greatly reduced premaxillary ascending processes in adults; dumbbell shaped rostral cartilage; pectoral fins lowset and rays increased to 20–23; vertebrae increased to 45–54; supraorbital pores reduced; intrafollicular gestation; formation of spermatozeugmata; gonopodium formed principally from anal rays 3 through 9; Node D: gonopodium formed principally from anal rays 3, 6, and 7; other anal rays undergo degeneration; tubular gonopodium lacks scales; embryo receives nourishment via ovarian flaps; tricuspid outer jaw teeth in adults; Node E: greatly expanded premaxillary ascending processes; no rostral cartilage; five or six rows of tricuspid inner jaw teeth; fleshy sheath over urogenital opening in females; males with large anal papilla; preopercular pores covered with enlarged scales; males with from four to five precaudal bars.

with an expanded distal arm; a parasphenoid with an expanded anterior arm; dorsal process of the maxilla with a distinct lateral indentation; an elongate retroarticular; and a pouch created by scales surrounding the urogenital opening of females.

*Jenynsia, Anableps,* AND *Oxyzygonectes*: These three genera (fig. 78) share enlarged epiotic and supraoccipital processes, and outer and inner jaw teeth with lateral cusps in at least embryos and juveniles. A third possible derived character is laterality, expressed as a shift in the gonopodium (in the case of *Anableps* and *Jenynsia*) or the genital papilla (in the case of *Oxyzygonectes*) to either the left or the right.

*Anableps* and *Jenynsia* are hypothesized close relatives (fig. 79) based on their sharing specializations of the gonopodium and gonopodial suspensorium. The thickened and elongated anal rays are twisted around each other and covered by a fleshy tube. The sperm duct enters the tube at the anterior base of the anal fin and opens to the outside at the distal tip of the gonopodium which, in turn, is offset to either the left or the right of the midline, whereas the expanded proximal radials are offset to either the left or right of the vertebral column.

Females of *Jenynsia* and *Anableps* do not have a complete pouch of scales surrounding the urogenital opening. Instead, there are just one or a few scales covering the left or the right side of the opening defining a female as either dextral or sinistral, respectively.

The pigmentation pattern of several species of *Jenynsia* (e.g., *eigenmanni*) closely approaches that of *Anableps microlepis* (von Ihering, 1931). On the sides of the body are several rows of dashes of dark pigment over a pale yellow-green background. If the very regular pattern of *A. dowi* (as shown in Miller, 1979) consisting of a longitudinal yellow stripe on a dark dorsal surface and light ventral surface is defined as derived for that species, then *Jenynsia* and *Anableps* share some derived features of color patterns.

*Jenynsia* has a unique formation and development of the rays of the gonopodium. The principal rays of the gonopodium (3, 6, and 7) are elongated and elaborated. All other anal rays undergo degeneration; they are weakly formed and may easily be reported as absent in a cursory examination of the fin. In addition, the outer covering of the gonopodial tube is scaleless, whereas in *Anableps* it is fully scaled. If the presence of scales is primitive in the development of the gonopodial tube, then their absence in *Jenynsia* is derived.

The development of *Jenynsia* embryos is also unique in the formation of the large ovarian flaps which enter the pharyngeal and buccal cavities and are believed to supply nourishment to developing embryos.

In addition, the species of *Jenynsia* may be identified by their outer tricuspid teeth in adults. However, given that the character is expressed to some degree by *Anableps* and *Oxyzygonectes*, it should be considered primitive in *Jenynsia* and unicuspid teeth derived in *Anableps* and *Oxyzygonectes*.

The genus *Anableps* is defined by a number of derived features. The eyes are divided horizontally such that the fish has simultaneous aerial and aquatic vision (fig. 66). The frontals are greatly expanded dorsally to accommodate the enlarged orbits. The derived upper jaw of *Anableps* is also readily distinguished from all other cyprinodontiforms: there are weakly formed premaxillary ascending processes in adults; the remaining inner arms of the premaxillaries meet in the midline to form an arc. The ascending processes are present in embryos, therefore, the adults represent the derived condition of this state. Also, the rostral cartilage is dumbbell shaped.

The pectoral fins are set ventrally; internally this is effected by the radials being set ventrally. Pectoral rays are increased to 20–23, as opposed to 15 in *Jenynsia*.

The number of vertebrae is higher than in any other cyprinodontiform genus. The number ranges from 45 to 54 (Miller, 1979); whereas the highest number in other cyprinodontiforms is 41 in the genus *Lamprichthys*.

Gill rakers on the first arch are also increased to 21–30 compared to 10–11 in *Jenynsia*.

The supraorbital pore system is reduced from the general condition exhibited by *Jenynsia* to what have been identified as pores 3 and 4a and, 6 and 7; in addition, the head scales are arranged randomly, rather than in the primitive pattern.

Other derived characters related to reproduction distinguish the condition of viviparity in *Anableps* from that of *Jenynsia*, particularly the intrafollicular gestation and formation of sperm bundles in at least one species, *A. dowi*. These characters appear in other viviparous cyprinodontiforms and atherinomorphs, however, they must properly be regarded as independently derived in *Anableps* within this scheme.

The monotypic *Oxyzygonectes*, previously classified in the subfamily Fundulinae, exhibits a further derived state of the upper jaw exhibited by *Jenynsia* and the procatopines. The premaxillary ascending processes are greatly expanded in adults (fig. 35B). Also, no rostral cartilage has been found in the specimens examined. The difference of this condition relative to that in *Aplocheilus*, which also has expanded premaxillary ascending processes, may be observed by comparing the lateral views of jaws of the two. In *Aplocheilus* (fig. 27) the ascending processes are longer relative to the length of the dentary than they are in *Oxyzygonectes* (fig. 36) in which the ascending processes are shortened.

In addition there are five or six rows of tricuspid teeth on both the upper and lower jaws, three to four more rows than found in *Jenynsia* and *Anableps*.

Female *Oxyzygonectes* may be distinguished from males by the presence of a fleshy sheath covering the urogenital opening which itself is partially covered with scales. Males have a large anal papilla which, as stated, has been found in preserved specimens offset to the left or the right.

In life, males have from four to five precaudal bars and faintly mottled unpaired fins, as compared with the more drab females (Daniel Fromm, personal commun.). Background coloration in both males and females is a drab dark brown in preservation.

The preopercular sensory pore system is represented by the primitive number of seven pores. These are set apart and covered slightly by a series of large scales.

CLADISTIC SUMMARY OF *Jenynsia, Anableps,* AND *Oxyzygonectes*: Enlarged epiotic and supraoccipital processes, outer and inner jaw teeth with lateral cusps in at least embryos and juveniles, and sexual laterality

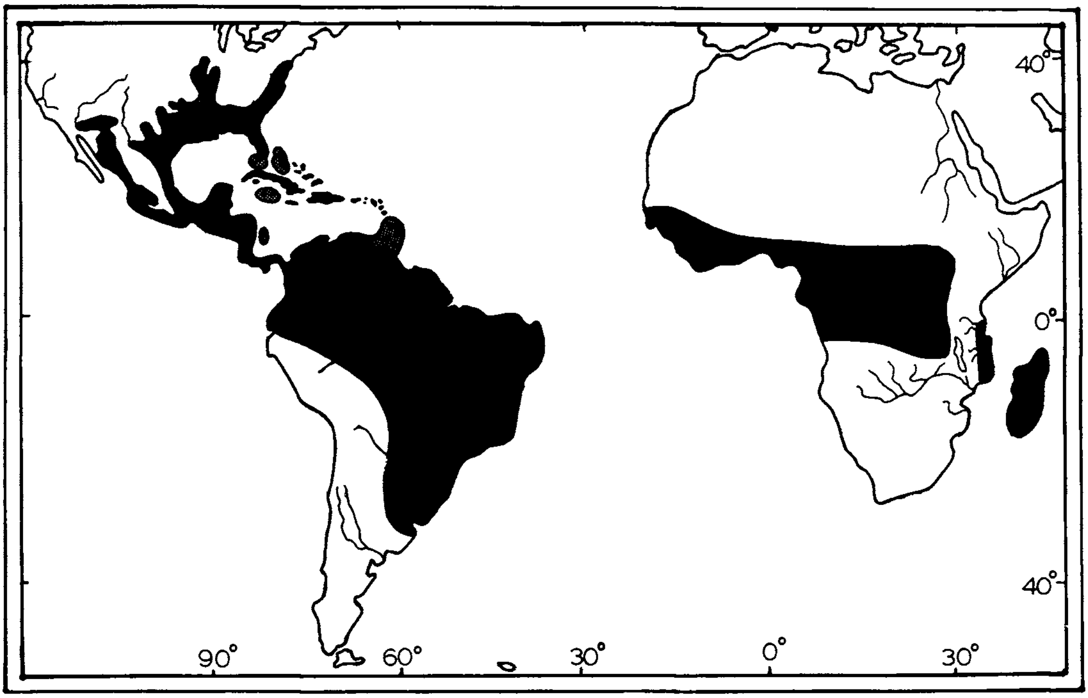

FIG. 80. Distributional limits of poeciliids, procatopines, *Fluviphylax* and *Pantanodon*. (After Rosen and Bailey, 1963; Turner, 1966.)

are shared by *Jenynsia, Anableps* and *Oxyzygonectes*.

*Jenynsia* and *Anableps* share derived characters of the gonopodium and gonopodial suspensorium (elaborate anal rays are twisted around each other and covered by a fleshy tube; the sperm duct enters the tube at the anterior base of the anal fin and opens to the outside at the distal tip of the gonopodium; gonopodium is offset to the left or right of the midline; proximal radials are offset to the left or right of the vertebral column) and of general pigmentation.

*Jenynsia* is defined by its unique form of the gonopodium (anal rays 3, 6, and 7 are elaborate, whereas all other anal rays undergo degeneration; and the gonopodium is scaleless) and development (ovarian flaps enter pharyngeal and buccal cavities to provide nourishment).

*Anableps* is defined by enlarged eyes, divided horizontally and accommodated by expanded frontals; weakly formed premaxillary ascending processes, and a dumbbell shaped rostral cartilage; pectoral fins set ventrally, and an increase in pectoral fin ray number to more than 20; reduced supraorbital pore system and head scales randomly arranged; formation of spermatozeugmata; intrafollicular gestation; and vertebrae increased to 45 or more.

*Oxyzygonectes* is defined by enlarged premaxillary ascending processes; the absence of a rostral cartilage; an increase in the number of rows of outer tricuspid teeth; males with anal papilla; females with anal pouch; males with four to five precaudal bars and faintly mottled unpaired fins; and large scales covering the preopercular canal.

POECILIIDS, *Fluxiphylax, Pantanodon* AND THE PROCATOPINES: This group (fig. 80) is hypothesized to be monophyletic by its members sharing five derived characters: (1) pectoral fins set high on the sides caused by the dorsal placement of the radials; (2) a derived hyoid bar with no ventral extension of

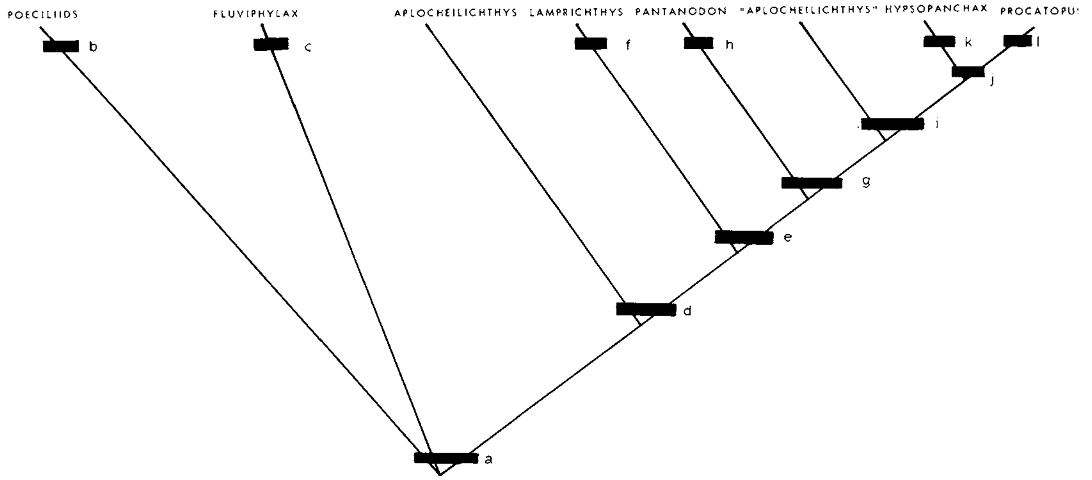

FIG. 81. Cladogram of relationships of poeciliids, procatopines, *Fluviphylax* and *Pantanodon*. Node A: pectoral fins set high on the sides, caused by the dorsal placement of the radials; hyoid bar with no ventral extension of the anterior ceratohyal accompanied by an expanded ventral hypohyal; pleural ribs on the first several hemal spines; anterior placement of the pelvic fins and their anterior migration during growth; recessed supraorbital pores 2b through 4a. Node B: gonopodium in males formed principally from anal rays 3, 4, and 5; modified hemal arches to provide support for the gonopodium; expansion of the inclinators of the anal fin to form a fan-shaped mass; modified pelvic fins of males; expansion of fourth epibranchial to become main support of the dorsal gill arch elements; exoccipital condyles absent; neural arches open. Node C: Enlarged eyes and reduced preorbital space; vomer unossified. Node D: mesethmoid cartilaginous. Node E: first postcleithrum absent; anal fin of 14 rays or more; expanded swimbladder extends beyond the first two to five hemal spines. Node F: increased number of vertebrae; ctenoid scales; caudal fin lyre-shaped; posttemporal with unossified lower limb. Node G: vomer tends to be unossified; no interarcual cartilage. Node H: tricuspid pharyngobranchial teeth; enlarged second pharyngobranchial toothplate; epibranchials one through three absent; hypobranchials absent; exoccipital condyles absent; neural arches of first vertebra expanded and applied to skull; fin spines present. Node I: robust dentary; articular reduced. Node J: reduction of alveolar arm; teeth extend to distal tip of premaxilla; reduction of the spatulate distal arm of the maxilla. Node K: Deep-bodied, caused by enlarged pleural ribs. Node L: Branchiostegal rays of males free from the membrane and extend posteriorly.

the anterior ceratohyal accompanied by the ventral hypohyal forming a bony cap over its anterior facet; (3) pleural ribs on the first several hemal arches; (4) the thoracic or subthoracic pelvic fins that migrate anteriorly during growth; and (5) recessed supraorbital sensory pores 2b through 4a. Also, Clausen (1959) described what he considered to be a behavioral convergence between the procatopines and the poeciliid subfamily Poeciliinae. This included an encounter in which the male "dances" before the female, spreads his fins and moves backward and forward. He also noted similarities in shape and coloration, without qualification.

The interrelationships of the poeciliids and other genera included in this group (fig. 81) are considered tentative because of the nature of some evidence, as discussed below, the scarcity of some material (particularly of the genus *Pantanodon*) and the large number of species in a polyphyletic genus (*Aplocheilichthys*).

The poeciliid fishes are easily distinguished from the other fishes of this group by the presence of a gonopodium in males formed principally from rays 3, 4, and 5 of the anal fin, modifications of the hemal arches to provide support for the gonopodium, expansion of the inclinators of the anal fin to form a fan-shaped mass of muscles, and modifications of the pelvic fins of males and their inferred function during copulation.

Also, the dorsal gill arches express a derived character in the expansion of the fourth epibranchial to become the main support of the dorsal gill arch elements.

As discussed for aplocheiloid interrelationships, the polarity of sexual dimorphism related to size cannot be determined. However, it is generally true that among cyprinodontoids females are larger than males. This is the case for the poeciliids and is therefore considered primitive. Among the procatopines, *Fluviphylax* and *Pantanodon,* males are generally much larger than females. Given the general nature of this character among cyprinodontoids, it may only be interpreted as a secondarily derived character suggesting the close relationship of these three groups.

Another derived character which all three share is the absence of parietals. Parietals are absent from some derived poeciliids, however, they are present in *Tomeurus.* Therefore, their presence must be considered primitive for poeciliids.

The interrelationships of the poeciliids, *Fluviphylax,* and the procatopines and *Pantanodon* is depicted as a trichotomy (fig. 81). Larger males and absence of parietals suggest the close relationship of *Fluviphylax* to *Pantanodon* and the procatopines. However, the diminutive South American *Fluviphylax* has a derived resemblance to the poeciliid *Tomeurus* in two respects: (1) the dorsal fin is small, composed of just four to six rays and is set rather far back on the body, and (2) the pectoral fins are extremely reduced, being composed of just nine or ten rays.

A derived character of the procatopines and *Pantanodon* is the presence of a cartilaginous rather than an ossified mesethmoid. The mesethmoid is ossified in both *Fluviphylax* and the poeciliids.

The genus *Aplocheilichthys* as currently constituted is polyphyletic. It contains over 60 nominal species (Lazara, 1979). These species have been divided into the following genera and subgenera in addition to *Aplocheilichthys* Bleeker: *Micropanchax* Myers, and its subgenus *Lacustricola* Myers; *Congopanchax* Poll, *Poropanchax* Clausen, *Cynopanchax* Ahl, *Plataplochilus* Ahl, and *Platypanchax* Ahl.

*Platypanchax* is apparently closely related to another procatopine genus, *Hypsopanchax,* for reasons discussed below. The remaining genera and subgenera contain some species that possess characters derived for more exclusive groups of procatopines. (Specimens of *Cynopanchax* and *Plataplochilus* were not available for study.)

All species of *Aplocheilichthys* examined possess a cartilaginous mesethmoid, therefore, are properly included in the group. *Lamprichthys, Procatopus, Hypsopanchax, Hylopanchax, Platypanchax* and their included subgenera are distinguished from more primitive species of *Aplocheilichthys* by lacking the first postcleithrum as well as having an elongate anal fin of 14 rays or more, and an expanded swimbladder which extends beyond the first two to five hemal spines.

The first postcleithrum is present in *Aplocheilichthys spilauchena,* the type species, yet is lacking in *A. johnstoni.* It is present in *Poropanchax.*

Within this group of procatopines and *Pantanodon, Lamprichthys* may be considered the relatively primitive member since it possesses a fully ossified vomer and an interarcual cartilage, as does *A. spilauchena.*

The interarcual cartilage is absent, therefore, presumed lost in *Procatopus, Hypsopanchax, Pantanodon,* and *A. johnstoni.* Thus, members of the genus *Aplocheilichthys* are related at different levels of generality to the other procatopine genera.

It is proposed that the more derived members of the genus, of which *A. johnstoni* may be considered representative, be referenced by the genus "*Aplocheilichthys.*"

The state of the ossified versus unossified vomer is rather ambiguous. The vomer is fully ossified in the specimens of *Lamprichthys* examined. However, in the genus *Hypsopanchax,* one species, *platysternus,* has an ossified vomer, whereas another species, *zebra,* has an unossified vomer. Nonetheless these two species of are considered to be members of the same genus. Therefore, the character may be more properly characterized as the tendency to not ossify the vomer. The vomer is similarly unossified in *Fluviphylax,* therefore, this may be an additional derived character indicating *Fluviphylax* is more closely related to the procatopines and *Pantanodon* than to the poeciliids. The ambiguous nature of the character precludes this conclusion at this time, however.

The diminutive *Fluviphylax pygmaeus* is defined by its greatly enlarged eyes. This condition is accompanied by a reduced preorbital distance as well as a narrow rather than wide lacrimal.

The genus *Lamprichthys,* endemic to Lake Tanganyika is a pelagic cyprinodontiform. It is one of the largest members of the group, attaining a standard length of over 150 mm. Vertebrae typically number 41, whereas the average number for this group is 30.

Males are distinguished from females by the presence of distinct ctenoid scales.

A third derived character is the shape of the caudal fin. Typically in cyprinodontiforms, the caudal fin is rounded or truncate. In *Lamprichthys,* the upper and lower caudal fin rays are extended to form a lyre-shaped caudal fin. Internally the supports are typical of those for cyprinodontiforms, however.

A fourth derived character is a straight posttemporal. As in other groups with such posttemporals the ventral limb is represented by an unossified ligament.

Among the genera that lack a vomer and an interarcual cartilage, *Pantanodon* is defined by the following derived characters: tricuspid pharyngobranchial teeth, greatly enlarged second pharyngobranchial toothplate, outer pelvic rays of males curved and elongate, exoccipital condyles absent, neurapophyses of the first vertebra expanded and closely applied to the skull, fin spines present, the lacrimal reduced, and the absence of hypobranchials.

The remaining genera *"Aplocheilichthys," Procatopus, Hylopanchax,* and *Hypsopanchax* share an extremely robust lower jaw. The dentary (fig. 37) is greatly expanded medially, more so than in any other group of cyprinodontoids, while the retroarticular is reduced.

Within this group, *Procatopus, Hylopanchax,* and *Hypsopanchax* together are defined as monophyletic by the reduction of the alveolar arm of the premaxilla and the extension of teeth to near the distal tip (fig. 37). This is accompanied by a reduction in the spatulate distal arm of the maxilla, distinctive in other members of the larger group including *Jenynsia, Anableps,* and *Oxyzygonectes.*

The species of *Procatopus* exhibit a derived character by which they may be readily distinguished from all other cyprinodontoids. In males, the first two branchiostegal rays are prolonged and extend beyond the opercular margin (fig. 53). Clausen (1959) divided the species into two subgenera, *Procatopus* Boulenger and *Andreasenius* Clausen. The pelvic fins in members of *Andreasenius* are set farther back on the body than those of the subgenus *Procatopus.* However, both possess the distinctive branchiostegal ray character, therefore, *Andreasenius* is treated as a synonym of *Procatopus.* Similarly, the genus *Hylopanchax* Poll and Lambert comprising just one species, *silvestris,* also has prolonged branchiostegal rays; therefore, it is also considered to be a synonym of *Procatopus.* (Poll and Lambert [1965] considered it to be intermediate between *Hypsopanchax* and *Procatopus*; however, the presence of this derived character clearly indicates its closer relationship to *Procatopus.*)

*Hypsopanchax* is distinguished from all other procatopines by its deep abdominal keel effected internally by enlarged ribs. Based on its description, the sole species of the genus *Platypanchax* is placed in *Hypsopanchax*; however, specimens have not been examined.

CLADISTIC SUMMARY OF POECILIIDS *Fluviphylax, Pantanodon,* AND PROCATOPINES: This group is defined by five derived characters: (1) pectoral fins highset, caused internally by dorsally placed radials; (2) ventral hypohyal forming a bony cap over the anterior facet of the anterior ceratohyal; (3) pleural ribs on the hemal arches; (4) thoracic or subthoracic pelvic fins which migrate or are inferred to migrate in ontogeny from a more posterior position; and (5) recessed supraorbital pores 2b through 4a.

The poeciliids, *Fluviphylax* and the procatopines and *Pantanodon* form an unresolved trichotomy. *Fluviphylax* and *Tomeurus* share a dorsal fin of four to six rays set far back on the body, and pectoral fins of just nine or 10 rays. *Fluviphylax* shares an absence of parietals and the condition of males larger than females with *Pantanodon* and the procatopines.

The poeciliids are defined by the following derived characters: internal fertilization by a gonopodium formed principally from anal rays 3, 4, and 5; modified hemal arches providing support for the gonopodium; expanded inclinators of the anal fin; modified pelvic fin rays in males; expansion of the fourth epibranchial to become the main support of the dorsal gill arch elements; exoccipital condyles absent, and neural arches open, not forming a spine.

*Fluviphylax* is defined by enlarged eyes and reduced preorbital space, as well as a possibly secondarily derived unossified vomer.

The procatopines and *Pantanodon* are defined by a cartilaginous mesethmoid.

*Aplocheilichthys* is polyphyletic as currently constituted. The genus is maintained to comprise the most primitive procatopines. The more derived members of the genus, referred to the genus "*Aplocheilichthys*" share three derived characters with the remaining procatopine genera: absence of the first postcleithrum; anal fin rays increased to 14 or more; and a swimbladder extending beyond the first two hemal spines.

*Lamprichthys* is defined by four derived characters: increased number of vertebrae; ctenoid scales; a lyre-shaped caudal fin; and, a posttemporal with a ligamentous ventral limb.

The genera "*Aplocheilichthys*," *Procatopus, Pantanodon,* and *Hypsopanchax* together are defined by a lack of the interarcual cartilage, and the tendency for the vomer to be unossified.

*Pantanodon* is defined by seven derived characters: tricuspid pharyngobranchial teeth; enlarged second pharyngobranchial toothplate; epibranchials one through three absent; hypobranchials absent; exoccipital condyles absent; neural arches of first vertebra expanded and applied to the skull; and fin spines present.

"*Aplocheilichthys*," *Procatopus* and *Hypsopanchax* all have a robust dentary and reduced articular.

*Procatopus* and *Hypsopanchax* have a reduced alveolar arm of the premaxilla, with teeth extending to its distal tip, and a reduction of the distal arm of the maxilla.

*Procatopus* is defined by several branchiostegal rays free from the branchiostegal membrane and extending posteriorly in males. *Hylopanchax* is treated as its junior synonym.

*Hypsopanchax,* of which *Platypanchax* is considered a junior synonym, is defined by its deep abdominal keel.

The two nominal genera *Cynopanchax* and *Plataplochilus* were not examined, and are simply listed in the systematic accounts.

GROUP G: The members of this group share the following derived characters: lateral ethmoid expanded medially and oriented so that it lies roughly perpendicular to the frontal; reduced autopterotic fossa; and inclinators of the anal fin greatly enlarged.

*Empetrichthys, Crenichthys,* AND THE GOODEIDAE: The three taxa (fig. 82) share four derived characters: (1) the first two to seven middle anal radials are fused to the proximal radials; (2) dorsal processes of the maxillaries are greatly reduced; (3) the distal arm of the premaxilla is straight, and (4) the articular is reduced.

*Empetrichthys* and *Crenichthys* are hypothesized to be sister taxa (fig. 83) based on their lack of pelvic fins and fin supports, and the derived shape of the first epibranchial.

*Empetrichthys* Gilbert is distinguished from *Crenichthys* Hubbs as well as other cyprinodontiform genera by its enlarged inferior pharyngeals as figured by Uyeno and

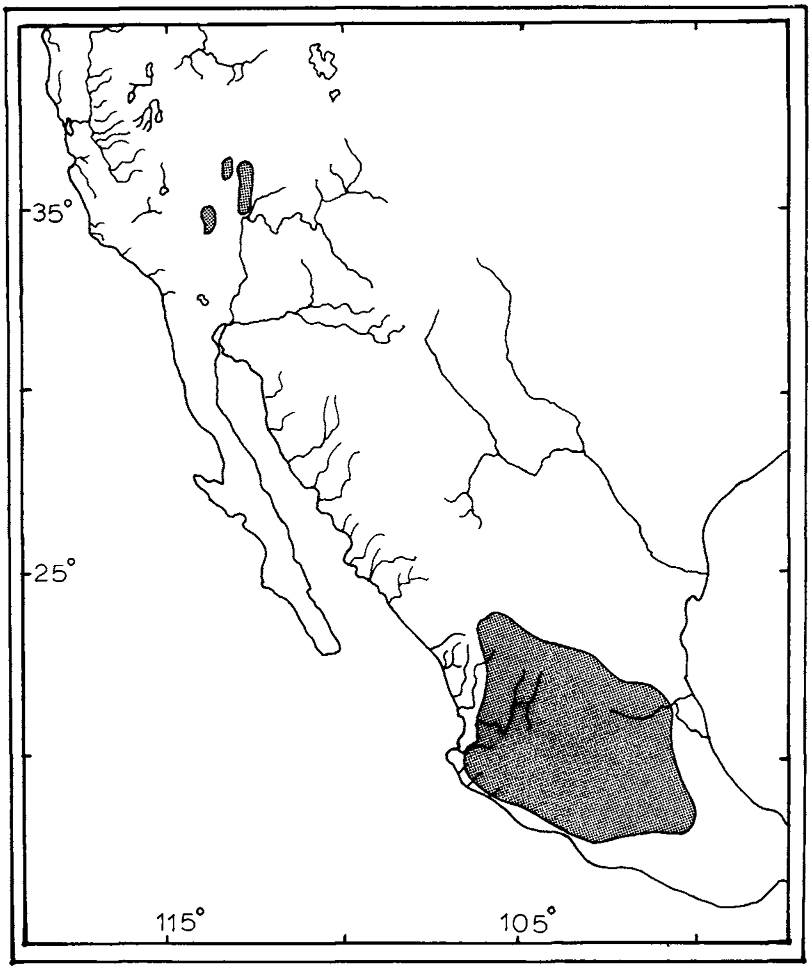

FIG. 82. Distributional limits of goodeids, *Empetrichthys* and *Crenichthys*. (After Miller and Fitzsimons, 1971; Miller, 1948.)

Miller (1962). It comprises two Recent species, *Empetrichthys merriami* (which is reportedly extinct) and *E. latos* which is divided into three subspecies. The genus name, meaning "fish with rocks within" refers to the enlarged molariform pharyngeal teeth found in *merriami,* the type species. Uyeno and Miller (1962) illustrated these elements for both species indicating that the teeth were only slightly enlarged in *latos*. However, the large conical teeth of both are unique among cyprinodontiforms. (A defining character of the cyprinodontine genus *Cualac* is the dense conical inferior pharyngeal teeth, fig. 84; however, these are much smaller than those in *Empetrichthys*.)

*Crenichthys* is readily distinguished by its unique arrangement of outer jaw teeth (fig. 33C). There is one large outer row of bicuspid teeth and several scattered inner rows of unicuspid teeth. Replacement teeth are prominent on the outer surface of the premaxilla and dentary. A similar arrangement is found in several goodeid genera (e.g., *Skif-*

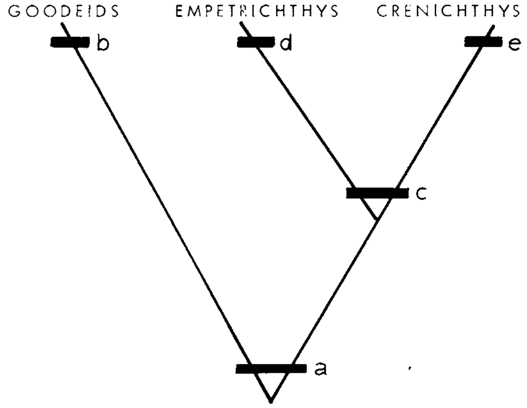

FIG. 83. Cladogram of relationships of goodeids, *Empetrichthys,* and *Crenichthys.* Node A: first two to seven middle anal radials absent or fused to proximal radials; distal arm of the premaxilla straight; dorsal process of the maxillaries greatly reduced; articular reduced. Node B: viviparous; first five to seven anal rays of males unbranched, shortened and set off from the rest of the anal fin by a notch; first anal ray rudimentary in males; muscular urogenital organ in males; trophotaeniae on embryos; ovary with ovigerous tissue partly or completely eliminated from ovarian walls. Node C: No pelvic fins or fin supports; Y-shaped first epibranchial. Node D: enlarged outer teeth; enlarged pharyngeal teeth; fleshy bases of dorsal and anal fins. Node E: Bicuspid outer teeth; high number of gill rakers on first arch.

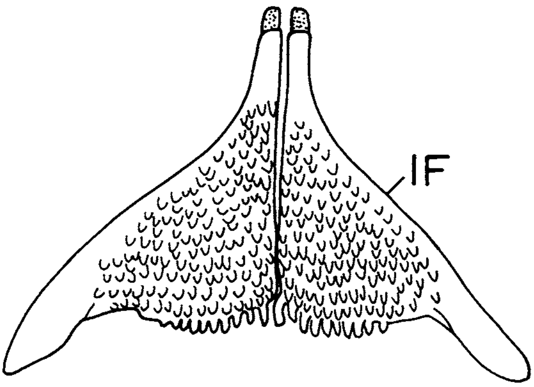

FIG. 84. Diagrammatic representation of inferior pharyngeals of *Cualac tessellatus.* Cartilage is stippled.

*fia* and *Zoogoneticus*); however, a close relationship of *Crenichthys* to the goodeids is not postulated on the basis of such a character. A proposed close relationship of *Crenichthys* to some more derived group of goodeids would render the goodeids as now constituted polyphyletic and such a conclusion is not supported. In addition, the genus is distinguished from *Empetrichthys* by its high number of gill rakers on the first arch which is 20 or more as opposed to 12–13 in *Empetrichthys.* The latter genus is further distinguished by having a fleshy base of the anal fin, whereas the base is fully scaled in *Crenichthys.*

The goodeids are defined as a monophyletic group by the following derived reproductive characters: the first five to seven anal rays of the male unbranched, shortened and set off from the rest of the fin by a notch; first anal ray rudimentary in adult males; a muscular urogenital organ or pseudophallus present in males; trophotaeniae of either a rosette or ribbon-like configuration in all but one species, and ovaries united medially with ovigerous tissue partly to completely eliminated from ovarian walls.

CLADISTIC SUMMARY OF *Empetrichthys, Crenichthys,* AND THE GOODEIDAE: This group is defined by four derived characters: first two to seven middle anal radials absent or fused to proximal radials; distal arm of the premaxilla straight; dorsal processes of the maxillaries greatly reduced; and, a reduced articular.

*Empetrichthys* and *Crenichthys* both lack pelvic fins and fin supports, and also share a derived form of the first epibranchial.

*Empetrichthys* is defined by enlarged outer and pharyngeal teeth, and fleshy bases of the dorsal and anal fins.

*Crenichthys* is defined by bicuspid outer teeth, and an increase in the number of gill rakers on the first arch.

The viviparous goodeids are defined by the following reproductive characters: first five to seven anal rays of male unbranched, shortened and set off from the rest of the anal fin by a notch; first anal fin ray rudimentary in males; muscular urogenital organ, termed a pseudophallus, in males; embryos with intestinal outpocketings, termed trophotaeniae; and, ovaries with ovigerous tissue partly to completely eliminated from ovarian walls.

GROUP I: The genera in this group share three derived characters: (1) the dorsal process of the maxillaries are expanded medially, nearly meet in the midline, and have a distinct groove; (2) the lateral arm of the maxilla is robust (fig. 42); and (3) the toothplate of the fourth pharyngobranchial is greatly reduced.

*Cubanichthys* AND *Chriopeoides*: These two monotypic genera are hypothesized to be sister taxa since they share a supraoccipital crest, an elongate dorsal process of the autopalatine, a supraorbital sensory pore pattern consisting of a large third pore, and a posttemporal lacking an ossified ventral limb. Thus, *Chriopeoides* Fowler, the younger name is treated as a junior synonym of *Cubanichthys* Hubbs.

GROUP J: Members of this group share the following derived characters: uniserial outer jaw teeth; second pharyngobranchial offset to the third; parietals absent; Meckel's cartilage expanded posteriorly; and the transverse processes of the vertebrae reduced and cup-shaped.

*Orestias* AND THE ANATOLIAN CYPRINODONTINES: The Andean *Orestias* (fig. 85) shares with the cyprinodontines of the Old World (fig. 86) a medial extension of the dentary which is enlarged in *Orestias* to form a bony shield in the upturned lower jaw.

The mesethmoid is cartilaginous in all specimens of Anatolian cyprinodontines examined in all four nominal genera: *Aphanius* Nardo, *Aphaniops* Hoedeman, *Kosswigichthys* Sozer, and *Anatolichthys* Kosswig and Sozer. It is ossified in all specimens of *Orestias* examined. However, the uniquely derived status of the cartilaginous mesethmoid is refuted in the analysis of other characters present in these five nominal genera.

*Aphanius* is nonmonophyletic and is only defined by a set of primitive characters: ossified interhyal; body fully scaled; posttemporal forked; urohyal not embedded, jaw not upturned (as discussed for *Orestias* and *Aphanius mento*); and the dermosphenotic present and with a distinct trough for the sensory canal.

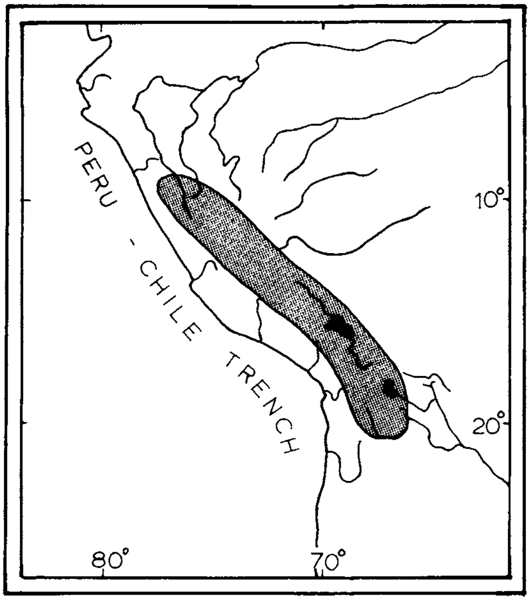

FIG. 85. Distributional limits of *Orestias*.

In *A. mento,* as well as in *Orestias, Kosswigichthys,* and *Anatolichthys,* the interhyal is cartilaginous and the urohyal is embedded as the lower jaw is set at an angle almost perpendicular to the body axis. In addition, there is the distinctive neuromast pattern on the dorsal surface of the head shared by the species of *Aphanius* related to *mento* and *Orestias*. The pattern is only weakly exhibited by the genus *Anatolichthys* and not at all in *Kosswigichthys* which lacks scales altogether.

Species of *Orestias* and those of *Anatolichthys* and *Kosswigichthys* are hypothesized to form a monophyletic group within this assemblage (fig. 87). They have in addition to the derived characters they share with *A. mento,* the following: the ventral limb of the posttemporal is represented by an unossified ligament; there is a reduction or total absence of scales (Ermin, 1946); and, the number of vertebrae is increased to 28 or more, as opposed to the general number of 24 found among the species of *Aphanius, Aphaniops,* and other cyprinodontines, as

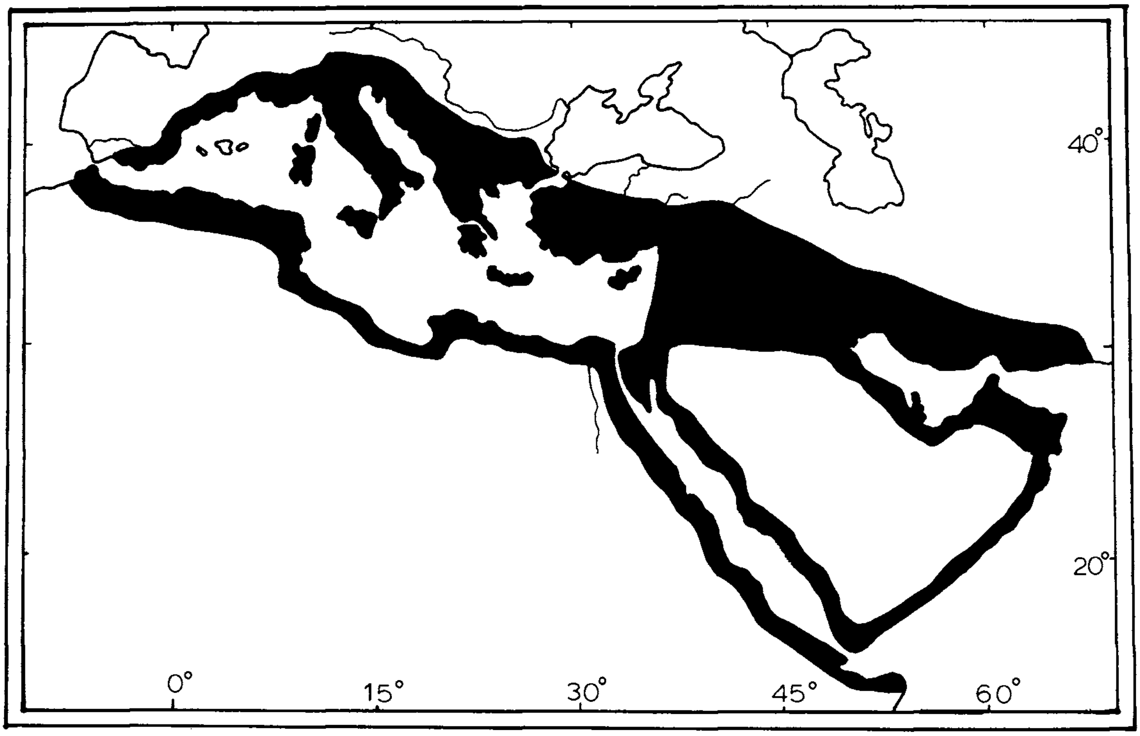

FIG. 86. Distributional limits of Anatolian cyprinodontines.

well as in *Cubanichthys*. The type species of *Aphanius*, *A. fasciatus*, is considered a primitive member of the Anatolian cyprinodontines. I propose to reference derived species as "*Aphanius*."

*Orestias* has the following derived characters: no vomer, no pelvic fins or fin supports, and no first postcleithrum.

The absence of a dermosphenotic supports the monophyly of, and hence, the synonymy of *Anatolichthys* in *Kosswigichthys*.

CLADISTIC SUMMARY OF *Orestias* AND THE ANATOLIAN CYPRINODONTINES: This group is defined by an expanded medial process of the dentary.

*Aphanius* is polyphyletic; within a phylogeny of the group, its derived members are referred to the genus "*Aphanius*."

"*Aphanius*" and the nominal genera *Kosswigichthys*, *Anatolichthys*, and *Orestias* share a cartilaginous interhyal; an embedded urohyal and lower jaw at nearly a right angle to the body axis; and a derived neuromast cephalic sensory pattern.

*Kosswigichthys*, *Anatolichthys*, and *Orestias* have a posttemporal with a ligamentous lower limb, a reduction or absence of scales, and an increase in the number of vertebrae to 28 or more.

*Anatolichthys* is treated as a junior synonym of *Kosswigichthys* which is defined by the absence of the dermosphenotic.

*Orestias* has no vomer, no pelvic fins or fin supports, and no first postcleithrum.

NEW WORLD CYPRINODONTINES: New World cyprinodontines (of the nominal genera *Cyprinodon* Lacépède, *Megupsilon* Miller and Walters, *Cualac* Miller, *Floridichthys* Hubbs, *Jordanella* Goode and Bean, and *Garmanella* Hubbs) are hypothesized to form a monophyletic group of genera based on their sharing a derived form of the attachment of the first vertebra to the skull. This is characterized by the loss of exoccipital

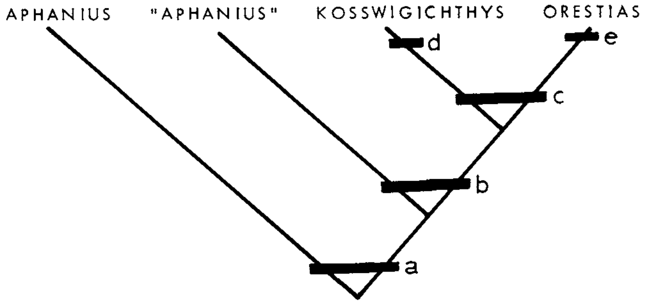

FIG. 87. Cladogram of relationships of *Orestias* and the Anatolian cyprinodontines. Node A: medial extension of dentary. Node B: interhyal cartilaginous; urohyal embedded and lower jaw nearly at right angle to body axis; neuromast sensory pore pattern. Node C: posttemporal lacks ossified lower limb; reduction or absence of scales; increase in number of vertebrae to 28 or more. Node D: loss of the dermosphenotic. Node E: no vomer; no pelvic fins or fin supports; no first postcleithrum.

condyles, the supraoccipital forming the dorsal wall of the foramen magnum rather than being excluded from it, and neurapophyses of the first vertebra angled anteriorly and firmly applied to the skull. In addition, the pharyngobranchial teeth are arranged in discrete rows.

The taxonomy of the New World cyprinodontines has been dominated by the naming of monotypic taxa which in some way depart from the general form of *Cyprinodon*. This genus currently comprises 36 species and subspecies (Lazara, 1979), whereas all the rest are monotypic.

Interrelationships of New World cyprinodontines are summarized in the cladogram of figure 89; their distribution in figure 88.

*Garmanella* is treated as a junior synonym of *Jordanella*. Both share elongate dorsal fins of 15 rays or more. They also both possess a discrete blotch at midbody and a black suborbital bar.

*Megupsilon aporus* was originally distinguished from all other species of the group by its possession of an enlarged Y-chromosome in the male, a sexually dimorphic chromosome number, the absence of pores in the cephalic sensory pore system, blackened scales on the sides of the body of breeding males, also lack a terminal band on the caudal fin, and not present in all *Cyprinodon* (Miller and Walters, 1972). Several breeding characteristics reportedly differ from those of *Cyprinodon*.

The position of *Megupsilon* in a phylogeny of all New World cyprinodontines is unresolved. *Megupsilon* lacks pelvic fins and fin supports, as do several species of *Cyprinodon*. Miller (1956) stated that *Cyprinodon* alone possessed an enlarged humeral scale; however, the variability of the size of such a scale in *Cyprinodon* and other genera precludes the use of this character for defining *Cyprinodon* as a monophyletic genus. *Cyprinodon* does have an enlarged extension of the scapula (fig. 8B). The scapula of *Megupsilon* is slightly enlarged, whereas that of *Jordanella, Floridichthys,* and *Cualac* is even less so.

Some *Cyprinodon* and *Jordanella floridae* have a thickened first dorsal ray that resembles a spine. The absence of a spine in *Jordanella* (*Garmanella*) *pulchra* suggests that this character is derived for some larger group. Thus *Megupsilon* is parsimoniously assessed as forming an unresolved trichotomy with *Cyprinodon* and *Jordanella* (fig. 89). It shares the absence of pelvics with *Cyprinodon* and the midlateral blotch with *Jordanella*.

*Floridichthys* and *Cualac* have an enlarged element in the position of the first pharyngobranchial. *Floridichthys* has an actual toothplate with a patch of teeth, whereas in *Cualac* the element is cartilaginous and devoid of teeth.

*Floridichthys* is unique among cyprinodontines in having a pectoral fin of 18 to

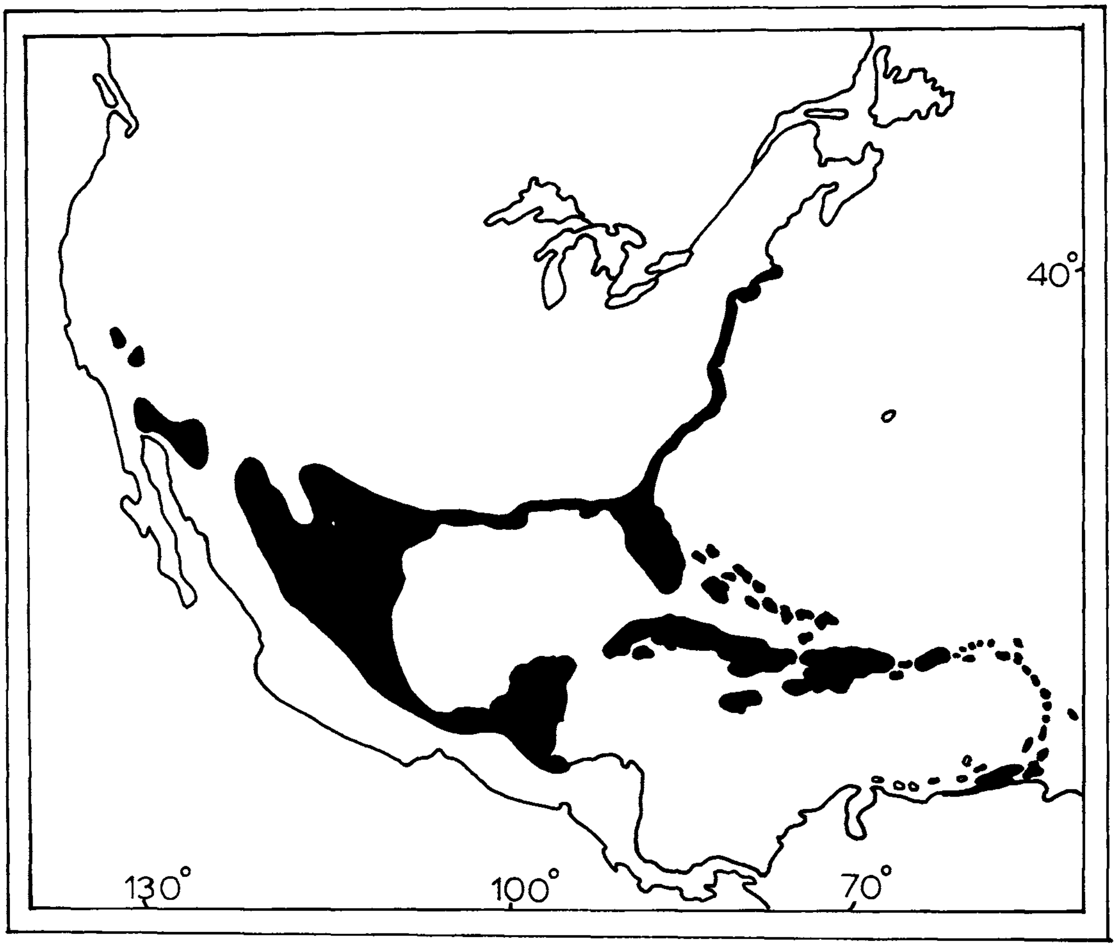

FIG. 88. Distributional limits of New World cyprinodontines.

20 rays, whereas *Cualac* has the typical lower range of 11 to 13.

*Cualac* is defined by expanded inferior pharyngeals (fig. 84) and their close-set, villiform teeth, as well as an increase in the number of gill rakers on the first arch to 17.

It could be argued that all New World cyprinodontines should be placed in one genus. However, since monophyletic groups of species can be defined, it is suggested that they be recognized until a phylogenetic analysis of all species is presented.

CLADISTIC SUMMARY OF NEW WORLD CYPRINODONTINES: New World cyprinodontines share the following derived characters: no exoccipital condyles; neural arches of the first vertebra open and applied to the skull; supraoccipital included in the formation of the foramen magnum; and, pharyngobranchial teeth arranged in discrete rows.

*Garmanella* is treated as a junior synonym of *Jordanella* which is defined by a dorsal fin with more than 15 rays, and a suborbital bar.

*Megupsilon* is defined by an enlarged Y-chromosome in males; sexually dimorphic chromosome number; and no cephalic sensory pores.

*Cyprinodon* is tentatively defined by an enlarged scapular process; yet, it is stressed that this genus is probably polyphyletic.

*Megupsilon, Jordanella,* and *Cyprinodon*

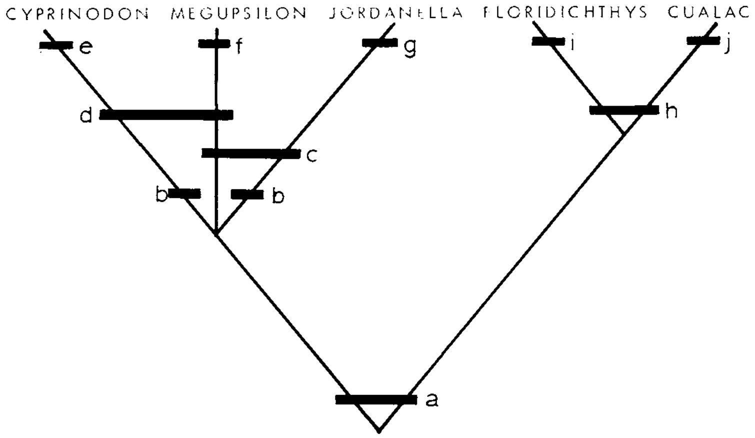

FIG. 89. Cladogram of relationships of New World cyprinodontines. Node A: no exoccipital condyles; neural arches of first vertebra angled anteriorly and applied to skull; supraoccipital included in formation of foramen magnum; pharyngobranchial teeth arranged in discrete rows. Node B: first dorsal spine often present. Node C: Dark, midlateral blotch. Node D: Pelvic fins and fin supports often absent. Node E: greatly enlarged scapular process. Node F: enlarged Y-chromosome in male, sexually dimorphic chromosome number; no cephalic sensory pores. Node G: elongate dorsal fin of more than 15 rays; suborbital bar. Node H: first pharyngobranchial present. Node I: first pharyngobranchial toothplate present with a patch of teeth. Node J: increased number of gill rakers on the first arch; inferior pharyngeal teeth packed closely together.

form an unresolved trichotomy. *Megupsilon* shares the absence of pelvic fins and fin supports with some species of *Cyprinodon,* whereas it shares the presence of a midlateral blotch with *Jordanella*. Some *Cyprinodon* and *Jordanella floridae* have a thickened first dorsal fin ray resembling a true spine.

*Cualac* and *Floridichthys* have a first pharyngobranchial element. *Floridichthys* has the inferred derived state, an ossified toothplate with a patch of teeth. The genus is also defined by a high number of pectoral fin rays (18–20). *Cualac* is defined by expanded inferior pharyngeals with close-set villiform teeth, and a high number of gill rakers on the first arch.

## CLASSIFICATION

The phylogenetic analysis just presented reveals that the present classification of cyprinodontiform fishes is not based on definable monophyletic groups. The purpose of a classification in a cladistic system is to summarize the hierarchy of relationships of the defined monophyletic groups of taxa (e.g., Nelson, 1973). It is also desirable but not necessary (see Farris, 1976) to give sister groups the same rank so that a cladogram or scheme of interrelationships may be inferred easily from a written classification.

At the same time some stability in nomenclature is desirable for reasons which are apparent. However, stability ceases to be desirable when a taxon as currently constituted, such as the Cyprinodontidae, is unnatural. Retaining the name to reference all oviparous killifishes (minus *Tomeurus*) would be to ignore the overwhelming evidence against the monophyletic nature of the group.

The system of interrelationships proposed in this study is far too complicated to be summarized easily using the existing system of five family names grouped together in one superfamily. Therefore, I propose that the rank of the superfamily be raised to an order, which shall be known as the Cyprinodontiformes Berg, a well-known and still widely used term for this group of fishes. In order that this classification conform to that for all members of the series Atherinomorpha, Rosen and Parenti (MS) have written a new classification of atherinomorph fishes.

Thus, the following classification of the cyprinodontiform fishes is proposed:

- Order Cyprinodontiformes Berg, 1940
  - Suborder Aplocheiloidei, new usage
    - Family Aplocheilidae Bleeker, 1860
      - Genus *Aplocheilus* McClelland, 1839
      - Genus *Pachypanchax* Myers, 1933b
      - Genus *Epiplatys* Gill, 1862
        - Subgenus *Lycocyprinus* Peters, 1868
        - Subgenus *Parepiplatys* Clausen, 1967
        - Subgenus *Pseudepiplatys* Clausen, 1967
        - Subgenus *Aphyoplatys* Clausen, 1967
      - Genus *Adamas* Huber, 1979
      - Genus *Aphyosemion* Myers, 1924b
        - Subgenus *Archiaphyosemion* Radda, 1977
        - Subgenus *Chromaphyosemion* Radda, 1971
        - Subgenus *Diapteron* Huber and Seegers, 1977
        - Subgenus *Kathetys* Huber, 1977
        - Subgenus *Mesoaphyosemion* Radda, 1977
      - Genus *Fundulopanchax* Myers, 1924b
        - Subgenus *Callopanchax* Myers, 1933c
        - Subgenus *Paraphyosemion* Kottelat, 1976
        - Subgenus *Paludopanchax* Radda, 1977
        - Subgenus *Gularopanchax* Radda, 1977
        - Subgenus *Raddaella* Huber, 1977
      - Genus *Nothobranchius* Peters, 1868
    - Family Rivulidae[1] Myers, 1925
      - Genus *Rivulus* Poey, 1860
      - Genus "*Rivulus*" (see pp. 483–484)
      - Genus *Trigonectes* Myers, 1925
      - Genus *Pterolebias* Garman, 1895
      - Genus *Rachovia* Myers, 1927
      - Genus *Neofundulus* Myers, 1924b
      - Genus "*Neofundulus*" (see pp. 489–490)
      - Genus *Austrofundulus* Myers, 1932
      - Genus *Cynolebias* Steindachner, 1876
  - Suborder Cyprinodontoidei
    - Section 1
      - Family Profundulidae Hoedeman and Bronner, 1951
        - Genus *Profundulus* Hubbs, 1924
    - Section 2
      - Division 1
        - Family Fundulidae Jordan and Gilbert, 1882
          - Genus *Plancterus* Garman, 1895
          - Genus *Fundulus* Lacépède, 1803
          - Genus *Adinia* Girard, 1859
          - Genus *Lucania* Girard, 1859
          - Genus *Leptolucania* Myers, 1924b
      - Division 2
        - Sept 1
          - Family Valenciidae, new family
            - Genus *Valencia* Myers, 1928b
        - Sept 2
          - Superfamily Poecilioidea, new usage
            - Family Anablepidae Garman, 1895
              - Subfamily Anablepinae Garman, 1895

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[1] Within the Lepidoptera, the subfamily Rivulinae was named by McDunnough (1938); the type genus is the North American moth *Rivula* Guenée [in Duponchel, 1835]. Following the International Code of Zoological Nomenclature, article 55a, this is a case of homonymy of family group names. The family group name is older in the Cyprinodontiformes and should be dropped from use in the Lepidoptera.

- Genus *Anableps* (Gronow) Scopoli, 1777
- Genus *Jenynsia* Günther, 1866

- Subfamily Oxyzygonectinae, new subfamily
  - Genus *Oxyzygonectes* Fowler, 1916

- Family Poeciliidae Garman, 1895
  - Subfamily Poeciliinae Garman, 1895
  - Subfamily Fluviphylacinae Roberts, 1970
    - Genus *Fluviphylax* Whitley, 1965
  - Subfamily Aplocheilichthyinae Myers, 1928a
    - Genus *Aplocheilichthys* Bleeker, 1863
      - Subgenus *Micropanchax* Myers, 1924a
      - Subgenus *Lacustricola* Myers, 1924a
      - Subgenus *Congopanchax* Poll, 1971
      - Subgenus *Poropanchax* Clausen, 1967
    - Genus *Lamprichthys* Regan, 1911
    - Genus "*Aplocheilichthys*" (see pp. 510–511)
    - Genus *Procatopus* Boulenger, 1904b
    - Genus *Hypsopanchax* Myers, 1924a
    - Genus *Pantanodon* Myers, 1955
    - Genus *Cynopanchax* Ahl, 1928
    - Genus *Plataplochilus* Ahl, 1928

- Superfamliy Cyprinodontoidea, new usage
  - Family Goodeidae Jordan, 1923
    - Subfamily Empetrichthyinae Jordan, Evermann and Clark, 1930
      - Genus *Empetrichthys* Gilbert, 1893
      - Genus *Crenichthys* Hubbs, 1932
    - Subfamily Goodeinae Jordan, 1923
  - Family Cyprinodontidae Gill, 1865
    - Subfamily Cubanichthyinae, new subfamily
      - Genus *Cubanichthys* Hubbs, 1926
    - Subfamily Cyprinodontinae Gill, 1865
      - Tribe Orestiini Bleeker, 1860
        - Genus *Orestias* Valenciennes, 1839
        - Genus *Kosswigichthys* Sozer, 1942
        - Genus *Aphanius* Nardo, 1827
        - Genus "*Aphanius*" (see pp. 522–524)
      - Tribe Cyprinodontini Gill, 1865
        - Genus *Cyprinodon* Lacépède, 1803
        - Genus *Megupsilon* Miller and Walters, 1972
        - Genus *Jordanella* Goode and Bean, 1879
        - Genus *Floridichthys* Hubbs, 1926
        - Genus *Cualac* Miller, 1956

Familiar group names have been retained only if they can be used in the same manner as in previous classifications, or, if the membership of such categories could be slightly expanded or contracted to include close relatives or eliminate unrelated taxa, respectively. An example in which the practice has been applied is in the family Poeciliidae. As previously defined, it included only those members which possessed a gonopodium in males formed principally from anal rays 3, 4, and 5. This group is retained here as the subfamily Poeciliinae, whereas the family Poeciliidae has been expanded to include the procatopines and *Pantanodon* (subfamily Aplocheilichthyinae), and *Fluviphylax* (subfamily Fluviphylacinae). The relationships of these three groups are expressed in the cladogram as an unresolved trichotomy, therefore, each of the three groups is given equal rank. Similarly, the family Goodeidae has traditionally been limited to the viviparous forms of the Mexican Plateau. The rank of this group of genera has been reduced to a subfamily, the Goodeinae, whereas the two genera proposed as its sister group, *Empetrichthys* and *Crenichthys*, are placed in the subfamily Empetrichthyinae. The family name Goodeidae is therefore used to encompass these two subfamilies.

Three informal categories (division, section, and sept) have been employed both to provide stability in the nomenclatorial scheme and also to minimize the number of empty categories. Thus, the genus *Profundulus*, represented as the primitive sister group of all other cyprinodontoids (classified here as the suborder Cyprinodontoidei) is placed in its own family, for the sake of tradition alone, the Profundulidae. However, rather than placing the family Profundulidae in its own superfamily, and similarly all other members of the suborder in another superfamily, I have elected to use the informal category of section for this purpose. Logically, there is no difference between the two approaches. However, the use of an informal category at this point and between the next two divisions of the suborder, leaves the category superfamily to reference those groups that contain more than one family. Thus, there is no alteration of the definitions of higher categories except in the cases where families contain just one genus, but the reason for this has already been stated.

The informal categories have not been named since their names would be trivial additions to the classification. For example, names of Section 2, Division 2 and Sept 2 would all have *Cyprinodon* as a root and some arbitrary ending. The names of Section 1, Division 1, and Sept 1 would all be modifications of the family names already included in them.

The generic groups within most families are those in current use. For the most part, their interrelationships and composition were not dealt with formally here. In the classification, the genera are simply listed; my expectation is that future work will succeed in classifying these groups in a hierarchy of suprageneric categories and that a revisor of the Rivulidae, for example, could very well introduce such categories into the system without altering the existing classification.

The reason for this expectation is that this classification system is designed to be both flexible and minimally disruptive to currently named monophyletic groups. As constituted, Section 1 of the suborder Cyprinodontoidei contains just one genus, *Profundulus*. Uyeno and Miller (1962) have remarked that some fossil specimens currently placed in the genus *Fundulus* may in fact be closely related to *Profundulus*. If so, another taxon (fossil or Recent) may be added to the system as a sister group of *Profundulus* without disrupting the existing higher categories. This type of change to a classification may be termed a "nondisruptive" change. In contrast, a "disruptive" change would occur in a classification if, for example, a family was found to be nonmonophyletic as in the case of the family Cyprinodontidae as the group name is used in the beginning of this study.

A "nondisruptive" change, by definition, may always be incorporated into a system with the use of informal categories if it is not possible to work it into the existing nomenclatorial system. A revisor of the subfamily Goodeinae (containing approximately 36 species in 16 genera) may wish to present, in the form of a cladistic classification, the interrelationships of the species with a redefinition of the genera. Below the subfamily level there are eight traditional hierarchical categories into which species may be grouped: species group, superspecies, subgenus, genus, supergenus, subtribe, tribe, and supertribe. A completely dichotomous sytem of interrelationships of 512 species could be accommodated within such a system. If there were not sufficient categories, informal categories could be applied. These may be named or numbered at the discretion of the revisor. In such cases, I propose that numbered informal categories be used in conjunction with traditional names. Most taxonomists work at the level of revising families or their subgroups. A revision of a superfamily is not frequently done in conjunction with the revision of an order, as is the present case, so that all ranks may be adjusted accordingly.

Ideally, we should have a system of nomenclature adaptable to all changes. A system of prefixes and suffixes could be agreed upon (as in Farris, 1976) to accomplish just this task; however, group names would quickly become unwieldy and therefore ignored in favor of the existing names. A group numbering system may be more usable. However, introduction at this time of a numerical classification, in stark contrast to all other existing classifications of fishes, would not have the desired effect. That is, it would not prompt the adoption of the new classification.

A "disruptive" change requires, by definition, a reclassification unless a group of taxa can be conveniently moved from one higher taxon to another. The taxonomy of many groups is in such a state; however, a more likely case is one such as that presented here. A "disruptive" change in the classification was judged to be necessary. Such decisions are always subjective. For example, mode of reproduction could have been judged as the single most important character to be expressed in a classification. If so, the traditional use of the term Cyprinodontidae would have been retained, and the genus *Tomeurus* moved from the Poeciliidae to that oviparous family. The philosophy adopted in this study, however, is not one of subjective weighting of characters for expression in a classification, but rather of the incorporation of all available evidence into a scheme of interrelationships which reflect the genealogy of the group under revision. It is concluded that the scheme presented here, in being rigorously cladistic, is a better estimate of the one true phylogeny of the cyprinodontiform fishes than others, past or current (Garman, 1895; Regan, 1911; Jordan, 1923; Hubbs, 1924; Myers, 1931, 1955; and Sethi, 1960).

## KEY TO GENERA AND SUPRAGENERIC CATEGORIES

The following key is provided to aid in identifying the generic and suprageneric categories of cyprinodontoid fishes. It is based on the cladogram of figure 9 and the cladograms of monophyletic groups; however, since the key is dichotomous, the more derived states of transition series could not be represented. In addition, categories referred to in the classification as subgenera are not represented since, for the most part, these are either paraphyletic assemblages or groups which have not been studied in detail. The key is presented in the hope that it will be useful in recognizing the major differences among groups many of which have long been confused.

1A Three basibranchials; metapterygoid present; a dorsal ray on each of the first two dorsal radials; dorsal hypohyal present; alveolar arm of premaxilla not strongly indented posteriorly (fig. 3A); autopalatine process small, not reaching quadrate (fig. 29); orbital rim attached on lower half of orbit; lacrimal narrow and twisted (fig. 12A); dentary not expanded medially (fig. 31C); rostral cartilage large and disc-shaped (fig. 4); ligament from the interior arms of the maxillaries to the rostral cartilage present; ethmomaxillary ligament present; meniscus between premaxillary ascending processes and interior arms of maxilla present; basihyal expanded anteriorly (fig. 10A); anterior arm of autopalatine straight (fig. 29); exoccipital and basioccipital condyles not reduced (fig. 26); pelvic fin supports set close together with medial processes reduced (fig. 10A) ..... ........... Suborder Aplocheiloidei 2A

2A Supracleithrum fused to posttemporal; first postcleithrum present; opercular and branchiostegal membrane not covered with scales; head-scales not arranged in circular pattern; preopercle without ventral expansion (fig. 30); dermosphenotic large, with distinct canal (fig. 17B); premaxillary ascending processes tapered posteriorly (fig. 4A, B, C); no flange on second pharyngobranchial at point of articulation of the interarcual cartilage (fig. 24) .......... Family Aplocheilidae 3A

3A Epipleural ribs not bifid; premaxillary ascending processes expanded posteriorly (fig. 4A, B); expanded coronoid process on dentary (fig. 27); no uncinate process on fourth epibranchial for articulation of third epibranchial (fig. 24A) ........ 4A

4A Posttemporal straight, lower limb not present; ocellus at anterior base of dorsal fin in at least females and juveniles; orbital rim indented under frontals; teeth on the second and third hypobranchials .... 5A

5A Posterior edges of scales in males stand away from body; hypural plates fused into

a hypural fan in adults; premaxillary ascending processes do not meet in the midline (fig. 4B) ........... *Pachypanchax*
(East Africa, Madagascar, and the Seychelles)

5B Scales of males close to body; hypural plates separate in adults, upper plate often divided in two (fig. 2D); premaxillary ascending processes meet and overlap in the midline (fig. 4A) .................. *Aplocheilus*
(Indo-Malaysian region)

4B Posttemporal forked; no ocellus at anterior base of dorsal fin; orbital rim not indented; no teeth on the second and third hypobranchials ................. *Epiplatys*
(West Central Africa)

3B First five or six epipleural ribs bifid; premaxillary ascending processes tapered posteriorly, but not expanded (fig. 4C); coronoid process on dentary not enlarged (fig. 31C); extension present on fourth epibranchial for articulation with third epibranchial (fig. 24B) ............. 6A

6A Dorsal origin posterior to anal origin; dorsal fin rays less than 14; swimbladder extends past the first two or three hemal arches ...................... *Aphyosemion*
(West and Central Africa)

6B Dorsal origin opposite that of anal, or more anterior; dorsal fin rays 14 or more; swimbladder does not extend past the hemal arches ......................... 7A

7A Interarcual cartilage attaches to bony flange on second pharyngobranchial (fig. 24A); preopercular canal represented by pores ................ *Fundulopanchax*
(Central Africa)

7B Interarcual cartilage attaches directly to cartilage of second pharyngobranchial (fig. 24B); preopercular canal represented by open groove .......... *Nothobranchius*
(West, Central and East Africa)

2B Supracleithrum not fused to posttemporal; first postcleithrum absent; opercular and branchiostegal membrane united and covered with scales; head scales small, in series around the central "A" scale (fig. 13E); preopercle with ventral expansion and obsolescent sensory pore canal (fig. 13D); dermosphenotic small, often without distinct sensory canal (fig. 17C); bony flange present on second pharyngobranchial at point of articulation of interarcual cartilage (fig. 6A) .. Family Rivulidae 8A

8A Interhyal ossified; all fins rounded; pelvic fin rays 6 ........................ *Rivulus*
(Caribbean, North, Middle and South America)

8B Interhyal cartilaginous; dorsal and anal fins elongate in males; pelvic fin rays 7 .. 9A

9A Pectoral rays not reaching base of pelvics; rostral cartilage not elongate ........................... "*Rivulus*"
(Caribbean, Middle and South America)

9B Pectoral rays extended, reaching to or beyond the base of the pelvic fins; rostral cartilage elongate (fig. 4D) ........ 10A

10A No vertical bar through eyes; origin of dorsal posterior to origin of anal; anal rays of females not thickened .............. 11A

11A Mouth cleft oblique, anterior ramus of premaxilla reduced (fig. 21); snout pointed; interarcual cartilage present ........................... *Trigonectes*
(Brazil, Paraguay, Bolivia)

11B Mouth cleft not oblique, anterior ramus of premaxilla not reduced (fig. 3A); snout not pointed; interarcual cartilage absent ......................... *Pterolebias*
(Brazil, Peru)

10B Vertical bar through eyes, often reaching top of head; thickened anal rays in females ........................ 12A

12A Dorsal fin not elongate, rays generally less than 14 ....................... 13A

13A Less than 32 scales in a lateral series .......................... *Rachovia*
(Coastal Ilanos of Colombia and Venezuela)

13B More than 34 scales in a lateral series ....................... *Neofundulus*
(Paraguay)

12B Dorsal fin elongate, rays greater than or equal to 14 ..................... 14A

14A First proximal anal radial present; teeth on fourth ceratobranchial not reduced; neural spine on first vertebra not enlarged .................... "*Neofundulus*"
(Paraguay)

14B First proximal anal radial absent; teeth on the fourth ceratobranchial reduced; enlarged neural spine on the first vertebra .............................. 15A

15A Heavily pigmented anal papilla; caudal fin finely scaled for more than one-third its length; preopercular canal open ......... ..................... *Austrofundulus*
(Coastal Ilanos, Colombia, and Venezuela)

15B Anal papilla bare or only lightly pigmented; caudal fin scaled only to its base; preopercular canal closed ...... *Cynolebias*
(Venezuela, Brazil, Argentina)

1B Two basibranchials; metapterygoid absent; one dorsal ray articulating with the first two dorsal radials; dorsal hypohyal absent; alveolar arm of premaxilla strongly indented posteriorly (fig. 3B); autopalatine process large, reaching quadrate (fig. 30); orbital rim free; lacrimal flat and wide (fig. 12C); dentary expanded medially (fig. 33); rostral cartilage reduced; no ligament from the interior arms of the maxillaries to the rostral cartilage; no ethmomaxillary ligaments; no meniscus between maxilla and premaxilla; basihyal narrow, not expanded anteriorly; anterior arm of autopalatine angled sharply (fig. 30); exoccipital and basioccipital condyles reduced; pelvic fin bases not set close together and medial processes not reduced (fig. 10B, C) ............ Suborder Cyprinodontoidei 16A

16A Premaxillary ascending processes flat and broad; inner arms of maxillaries united with large and rectangular rostral cartilage (fig. 5B); lateral ethmoids with anterior flanges (fig. 57A); autopterotic fossa enlarged (fig. 57A).. Family Profundulidae
*Profundulus*
(Highlands of western Middle America)

16B Premaxillary ascending processes narrow or absent; rostral cartilage small and disc-shaped or absent; inner arms of maxillaries not in direct contact with rostral cartilage; lateral ethmoids without anterior flanges (fig. 57B); autopterotic fossa not enlarged (fig. 57B)................ 17A

17A Interior arms of maxillaries directed anteriorly, often with pronounced hooks (fig. 34), no dorsal process directed over the premaxillary ascending processes; maxilla twisted, not straight (fig. 5C) ........................ Family Fundulidae 18A

18A Posttemporal forked; intestine convoluted ........................ *Plancterus*
(Central North America)

18B Posttemporal straight; intestine straight .................................. 19A

19A Second pharyngobranchial with expanded articular surface; epipleural ribs meet pectoral ribs rather than the parapophyses of the abdominal vertebrae ..... *Fundulus*
(North and Middle America)

19B Second pharyngobranchial without expanded articular surface; epipleural ribs meet distal tips of parapophyses of the abdominal vertebrae ...................... 20A

20A Epiotic processes present; supraoccipital canal system present between pores 1 and 7 ......................... *Lucania*
(East Coast of North America and Cuatro Cienegas Basin)

20B No epiotic processes; supraorbital canal system present between pores 6 and 7 21A

21A Body quadrangular; branchiostegal rays 5; first postcleithrum present; first pleural rib on parapophyses of first vertebra; no caudal or midbody ocellus ......... *Adinia*
(Florida to Texas)

21B Body elongate, not trapezoidal; branchiostegal rays 3; no first postcleithrum; first pleural rib on parapophysis of the second vertebra; an ocellus on the caudal peduncle and one at midbody ... *Leptolucania*
(Florida and Georgia)

17B Interior arms of maxillaries attenuate, directed medially, never with pronounced hooks; dorsal process directed over the premaxillary ascending processes, or process absent; maxilla straight, not twisted (fig. 35) ........................ 22A

22A Ascending processes of premaxillaries long and thin, not shortened; dorsal processes of maxillaries elongate (fig. 5D) .......................... Family Valenciidae
*Valencia*
(Spain, Italy and Corfu)

22B Ascending processes of premaxillaries shortened; dorsal processes of the maxillaries rounded when present ............ 23A

23A Distal arm of maxilla expanded; anterior arm of parasphenoid spatulate; lateral ethmoids not expanded, dorsal processes lie under frontals; premaxillary ascending processes with distinct lateral indentation (fig. 35); autopterotic fossa not reduced (fig. 16); inclinators of the anal fin not enlarged (fig. 72) .................. 24A

24A Dentary not enlarged; no pouch created by scales of female around anus and first few anal rays; no pectoral ribs on hemal spines; pectoral girdle set low on the sides, radials situated ventrally or posteriorly (fig. 8); pelvic fins not set forward; hyoid bar with ventral extension of anterior ceratohyal; enlarged epiotic and supraoccipital processes; outer teeth with distinct lateral cusps in embryos or juveniles ...... Family Anablepidae 25A

25A Tubular gonopodium associated with sperm duct in males formed from anal rays crowded together and twisted around each other; inner rows of jaw teeth unicuspidate or tricuspidate, in two uneven rows; adult males with gonopodium offset to left or right of midline; females with no pouch around urogenital opening or first few anal rays; females with one or a few scales on left or right side of urogenital opening ........... Subfamily Anablepinae 26A

26A Eyes normal; vertebrae 31; outer row of jaw teeth tricuspid; premaxillary ascending processes present; frontals flat, not expanded; tubular sperm duct not covered with scales; radials set posteriorly; anterior nares not tubular; supraorbital sensory pores represented by pores 1–2a, 2b–4a, and 4b–7; rostral cartilage round; gill rakers on first arch 10–11; gonopodium formed principally from rays 3, 6, and 7; sixth middle radial enlarged (fig. 68) ........................... *Jenynsia*
(Southern South America)

Eyes divided horizontally; vertebrae 45 or more; outer row of jaw teeth unicuspid in adults; premaxillary ascending processes absent in adults, weakly present in embryos; frontals expanded dorsally above orbit; tubular sperm duct covered with scales; radials set ventrally; tubular anterior nares; supraorbital pore system represented by pores 1–2, 3, 4a and 6 and 7; rostral cartilage dumbbell-shaped; gill rakers on first arch 21–30; gonopodium formed principally from anal rays 3–6; sixth middle radial not enlarged (fig. 67) ....................... *Anableps*
(Central and Southern South America)

25B No gonopodium; inner jaw teeth tricuspidate, set in numerous bands (fig. 36); scales covering preopercular canal; females with pouch over urogenital opening and first few anal rays ................ ........... Subfamily Oxyzygonectinae
*Oxyzygonectes*
(Pacific coast of Costa Rica)

24B Dentary enlarged (fig. 38C); pectoral rib on first hemal spine; pectoral girdle set high on the sides, radials situated dorsally (fig. 8); pelvic fins set forward, nearly under pectorals in most; hyoid bar without ventral extension of anterior ceratohyal; epiotic and supraoccipital processes not enlarged; outer teeth without lateral cusps ......... Family Poeciliidae 27A

27A Gonopodium in males, formed from anal fin rays 3, 4, and 5 associated with expanded anal radials and anteriorly porjecting hemal arches (fig. 65); males smaller than females; parietals present or absent .... ................ Subfamily Poeciliinae
(North, Middle and South America)

27B No gonopodium, anal fin normal; males larger than females; parietals absent ... 28A

28A Mesethmoid ossified; body fusiform; anal fin rays 7 or 8; dorsal fin rays 5 or 6; eye large in head, preorbital space narrow ...... ........... Subfamily Fluviphylacinae
*Fluviphylax*
(Amazon Basin)

28B Mesethmoid cartilaginous; body and peduncle compressed; anal fin rays 11 or more; dorsal fin rays 10 or more, eye with smaller preorbital space .................... ..... Subfamily Aplocheilichthyini 29B

29A First postcleithrum present; anal fin rays less than 14; swimbladder not extending past the first hemal arch.... *Aplocheilichthys*
(Central and Eastern Africa)

29B First postcleithrum absent; anal fin rays more than 14; swimbladder extending past first hemal arch ................. 30A

30A Interarcual cartilage present; posttemporal straight, without lower limb; vertebrae 41; vomer ossified; cteni on scales; caudal fin with upper and lower caudal fin extensions ...................... *Lamprichthys*
(Lake Tanganyika)

30B Interarcual cartilage absent; posttemporal forked; vertebrae less than 41; vomer ossified or not; scales not ctenoid; caudal fin rounded or truncate ............. 31A

31A Pharyngobranchial teeth tricuspid; three pelvic spines in males; enlarged second pharyngobranchial toothplate (fig. 45); outer pelvic fin rays of males curved and elongate; teeth on premaxilla do not extend distally; distal arm of premaxilla curved; exoccipital condyles absent; no neural spine on first vertebra, neurapophyses of first arch expanded ......... ........................ *Pantanodon*
(Dar es Salaam and Madagascar)

31B Pharyngobranchial teeth unicuspid; no spines present; second pharyngobranchial toothplate not enlarged; outer pelvic fin rays of males normal; exoccipital condyles present; neural spine on first vertebra .. 32A

32A Distal arm of premaxilla curved; teeth do not extend distally on the arm ........... ................. "*Aplocheilichthys*"
(Central Africa)

32B Distal arm of premaxilla straight; teeth extend distally along the arm ........ 33A

33A Deep-bodied; first two branchiostegal rays of males not free from branchiostegal membranes ............ *Hypsopanchax* (East Central Africa)

33B Not deep-bodied; first two branchiostegal rays of males free from branchiostegal membranes (fig. 53) ....... *Procatopus* (Central Africa)

23B Distal arm of maxilla not expanded; anterior arm of parasphenoid thin; lateral ethmoids expanded medially, dorsal process not under frontals; attenuate premaxillary ascending processes; autopterotic fossa reduced (fig. 57); inclinators of the anal fin enlarged (fig. 73) ................ 34A

34A First two to five middle anal radials absent; proximal anal radials of males crowded together; dorsal processes of maxilla greatly reduced, no groove; toothplate of fourth pharyngobranchial not reduced; distal arm of premaxilla straight (fig. 40); articular reduced (fig. 33) ............................. Family Goodeidae 35

35A Pelvic fins present; first epibranchial not Y-shaped; anal rays 2 to 7 of male shortened; first anal ray rudimentary; pseudophallus present ......... Subfamily Goodeinae (Mesa Central, Mexico)

35B No pelvic fins or fin supports; first epibranchial Y-shaped (fig. 47B); anal rays of males not shortened; first anal ray not rudimentary; pseudophallus not present ......... Subfamily Empetrichthyinae 36A

36A Outer teeth unicuspid; anal and dorsal fin bases fleshy; inferior pharyngeal teeth enlarged; gill rakers on first arch 12–13 ..................... *Empetrichthys* (Death Valley System)

36B Outer teeth bicuspid; anal and dorsal fin bases fully scaled; inferior pharyngeal teeth normal; gill rakers on first arch more than 20 ...................... *Crenichthys* (Eastern Nevada)

34B All anal radials present; groove in dorsal processes of maxillae, expanded medially nearly meeting in midline (fig. 41); toothplate of fourth pharyngobranchial reduced; distal arm of premaxilla curved (fig. 42) ........................ 37A

37A Supraoccipital crest enlarged (fig. 58); dorsal process of autopalatine elongate; parietals present; biserial outer teeth; second pharyngobranchial not reduced; Meckel's cartilage not expanded posteriorly (fig. 31C); transverse processes of vertebrae not reduced ..................................... Subfamily Cubanichthyinae *Cubanichthys* (Cuba and Jamaica)

37B Supraoccipital crest not enlarged; dorsal process of autopalatine short; parietals absent; uniserial outer jaw teeth; second pharyngobranchial greatly reduced (fig. 49); Meckel's cartilage expanded posteriorly (fig. 43A); transverse processes of vertebrae reduced and cup-shaped Tribe Orestiini 38A

38A Medial extension of the dentary (fig. 43A, B); neural spine on first vertebra; supraoccipital excluded from formation of foramen magnum; exoccipital condyles present; pharyngobranchial teeth randomly arranged ..................... 39A

39A Urohyal not embedded (fig. 13C); dermosphenotic not reduced ....... *Aphanius* (Mediterranean)

39B Urohyal embedded (fig. 14I); dermosphenotic reduced or absent ............ 40A

40A Interhyal ossified; body fully scaled; posttemporal with lower limb ossified; vertebrae 27 or less ........... "*Aphanius*" (Eastern Mediterranean, Iran and Turkey)

40B Interhyal cartilaginous; scales greatly reduced or absent; posttemporal straight, without lower limb; vertebrae more than 27 ............................ 41A

41A Pelvic fins present; vomer present; first postcleithrum present; dermosphenotic absent ................ *Kosswigichthys* (Fresh water lakes of Turkey)

41B Pelvic fins absent; vomer absent; no first postcleithrum; dermosphenotic greatly reduced ................... *Orestias* (Lakes of South American continental divide)

38B No anteriorly directed medial extension of dentary; neural arches of first vertebra applied to skull (fig. 62); no neural spine on first vertebra; supraoccipital bordering the dorsal wall of the foramen magnum; exoccipital condyles wanting; pharyngobranchial teeth arranged in discrete rows (fig. 49) ..... Tribe Cyprinodontini. 42A

42A First dorsal spine often present; dorsal ocellus often present in females; first pharyngobranchial absent .............. 43A

43A Dorsal fin with 14 or fewer rays; no suborbital bar; prominent scapular process ............................. 44A

44A Males without blackened scales on side;

pores present in cephalic sensory canal system; scapular process greatly enlarged (fig. 8B) .................. *Cyprinodon*
(North, Middle and South America)

44B Males with blackened scales on side; pores absent in cephalic sensory canal system; scapular process not enlarged ......... ......................... *Megupsilon*
(Nuevo Leon, Mexico)

43B Dorsal fin with more than 15 rays; suborbital bar present; scapular process not prominent ..................... *Jordanella*
(Florida and the Yucatan Peninsula south to Belize)

42B No dorsal spine; no dorsal ocellus; first pharyngobranchial present ........... 45A

45A First pharyngobranchial toothplate present with a patch of unicuspid teeth (fig. 50A); pectoral fin rays 18–20; inferior pharyngeals not expanded, teeth with slight shoulders; gill rakers on the first arch 9–10 ...................... *Floridichthys*
(Florida and the Yucatan Peninsula south to Honduras)

45B Cartilaginous first pharyngobranchial lacking teeth (fig. 50B); pectoral fin rays 11–13; inferior pharyngeals expanded, with closely set villiform teeth (fig. 84); gill rakers on the first arch 17......... *Cualac*
(San Luis Potosi, Mexico)

# SYSTEMATIC ACCOUNTS

## ORDER CYPRINODONTIFORMES BERG

DIAGNOSIS: Distinguished from all other atherinomorph fishes by the following derived characters: symmetrical caudal fin supported internally by one epural which mirrors in shape and position an opposing parhypural; premaxilla with a two-part alveolar process; first pleural rib arising on the parapophysis of the second vertebra rather than the third; interarcual cartilage arising from the base of the first epibranchial and attaching to the second pharyngobranchial; primitively lowset pectoral girdle with a large, scale-shaped first postcleithrum; and an extended developmental period.

DEFINITION: Typically small fishes, average adult 80–100 mm. SL; range approximately 8–300 mm. SL. Distribution pantropical and temperate North and Middle American, Eurasian, and Indo-Malaysian. Inhabitants generally of fresh water, although many members enter brackish water.

Markedly sexually dimorphic. Males and females of the same or unequal sizes. Males often brightly colored, with extensions of pelvic, dorsal, and caudal fin rays. Females usually drab, rarely with any brightly colored markings or fin extensions. Males with a gonopodium in three groups.

Body typically fusiform, rarely laterally compressed. Fins soft-rayed, rarely a spinous first dorsal or first three or four pelvic fin rays. Pectoral and pelvic fin position variable, pelvic fins and fin supports present or absent.

Caudal fin rounded or truncate, or with dorsal and ventral fin extensions in males. Caudal skeleton composed of one epural similar in shape and position to the opposing parhypural. Hypurals fused into two subequal dorsal and ventral segments, or the segments fused to form a hypural fan. In several species, upper hypural plate represented by two segments.

Infraorbital series represented by a lacrimal and dermosphenotic only. Vomer present or absent. Scales usually cycloid, sometimes ctenoid; body generally fully scaled; scales reduced on venter or totally absent in some members; head generally fully scaled; trunk lateral line represented by pitted scales. Cephalic lateral line system represented by canals, exposed neuromasts and pit organs.

Jaw teeth uni-, bi- or tri-cuspidate, in one outer and one to several inner rows, or in single outer row only.

Premaxillary ascending processes present or absent; when present, flat and broad, narrow and elongate or narrow and short. Rostral cartilage present as a large disc, reduced to a minute disc, or absent.

Interarcual cartilage from base of the first epibranchial to cartilage of second pharyngobranchial present or rarely absent; when present large and equal or one-half the length of the first epibranchial. Pharyngobranchial toothplates two, three, and four separate or, three and four fused; or all three fused to form one large toothplate; pharyngobranchial teeth unicuspid or tricuspid, often molariform.

Branchiostegal rays three to seven.

Scales in lateral series 24–96, vertebrae 24–54. Oviparous, ovoviviparous or viviparous. Developmental period generally of 10 days or longer. Annual, semiannual, or nonannual reproductive modes. Internal or external fertilization.

## SUBORDER APLOCHEILOIDEI

DIAGNOSIS: Distinguished from other cyprinodontiforms by the following uniquely derived characters: orbital rim attached at least on the lower half of the orbit, pelvic fin bases set close together with medial processes reduced, a broad anterior end of the basihyal, a narrow and twisted lacrimal associated with a narrow preorbital distance, and the posterior extension of the vomer dorsal to the parasphenoid; distinguished by the following derived characters considered to be convergent in other cyprinodontiforms: mesethmoid cartilaginous, tubular anterior naris, males always larger than females, and a reduced supraorbital sensory pore system.

COMPOSITION: Two families, Rivulidae Myers and Aplocheilidae Bleeker, as defined below.

DISTRIBUTION: Pantropical and Old World temperate Laurasian, one family (Rivulidae) New World, the other (Aplocheilidae) Old World, with distributions as detailed below.

### FAMILY APLOCHEILIDAE BLEEKER

Type Genus *Aplocheilus* McClelland, 1839.

DIAGNOSIS: Distinguished from all other Cyprinodontiformes in having the supracleithrum fused to the posttemporal; premaxillary ascending processes tapered posteriorly; basihyal reduced to a small triangular ossification; and the interarcual cartilage attaching directly to the lateral surface of the cartilaginous articular surface of the second pharyngobranchial.

COMPOSITION: Six recognized genera: *Aplocheilus* McClelland, *Epiplatys* Gill with four subgenera, *Pachypanchax* Myers, *Nothobranchius* Peters with four subgenera, *Adamas* Huber and *Aphyosemion* Myers with 11 subgenera.

DISTRIBUTION: (fig. 23) Old World; Africa south of the Sahara Desert from the lowlands of southern Mauritania in western Africa, south through Zaire; the northern limit the Niger River then east to western Sudan, south of the Ethiopian Highlands to western Somalia, southward to the coastal lowlands of South Africa; Madagascar; the Seychelles; Indian subcontinent and Sri Lanka (Ceylon), eastward through the Indo-Malaysian Archipelago to Java.

#### GENUS *APLOCHEILUS* MCCLELLAND

*Aplocheilus* McClelland, 1839, p. 301 (type species *Esox panchax* Hamilton-Buchanan, by original designation).

*Panchax* Cuvier and Valenciennes, 1846, p. 380 (type species *Esox panchax* Hamilton-Buchanan, by original designation).

*Haplochilus* Agassiz, 1846, p. 24 (proposed as an emendation of *Aplocheilus* McClelland).

ETYMOLOGY: *Aplocheilus* from the Greek *aplos,* meaning single or simple and *cheilus,* meaning lip, referring to the thin upper and lower jaw margins.

COMPOSITION: Five species: *panchax* (Hamilton-Buchanan), with seven nominal subspecies; *werneri* Meinken; *lineatus* (Cuvier and Valenciennes); *blocki* (Arnold); and *dayi* (Steindachner).

DIAGNOSIS: Distinguished from all other cyprinodontiforms by a derived upper jaw in which the premaxillary ascending processes overlap in the midline, and the lower jaw is greatly attenuated.

DEFINITION: Anal: iii, 12–iii, 13; Dorsal: ii, 6; Pelvic: 6; Pectoral: 14; Caudal: 5, 14, 5. Vertebrae: 13+14. Gill rakers on the anterior arm of the first arch: 12; Branchiostegal rays: 6. Scales lateral series: 25–31.

First pleural rib on parapophysis of second vertebra; parapophysis not reduced; a pleural rib often on first hemal spine; hypural plates divided, upper plate often divided in two. Epipleural ribs not bifid.

Anal fin not modified into a gonopodium; anal fin musculature unmodified; first proximal radial present; middle anal radials present.

Spermatozeugmata not formed; fertilization external; development nonannual; oviparous. Eggs round.

One dorsal ray articulating with each of the first two dorsal radials; dorsal fin on posterior third of body.

Autopterotic fossa normal; lateral ethmoid not expanded medially; not reaching parasphenoid; parasphenoid not expanded anteriorly; weakly formed supraoccipital and epiotic processes; neural spine on first vertebra; first vertebra articulates with skull via basioccipital and exoccipital condyles; supraoccipital excluded from formation of foramen magnum; parietals present; nasal not expanded medially.

Mesethmoid cartilaginous; medial processes of pelvic fin base and ischial process reduced; interarcual cartilage large, attaches laterally to second pharyngobranchial which lacks bony flange; basihyal broad anteriorly, triangular ossification posteriorly; tooth patches on second and third hypobranchials; teeth on fourth ceratobranchials; dorsal and ventral hypohyal present; anterior extension of anterior ceratohyal ventral to hypohyals; no uncinate process on fourth epibranchial to articulate with that of third; first epibranchial narrow at its base. Interhyal ossified; three ossified basibranchials. Vomer with posterior extension dorsal to parasphenoid.

Lacrimal narrow and twisted carrying distinct sensory canal; dermosphenotic and preopercular with distinct sensory canal; pectoral girdle lowset; first postcleithrum present; posttemporal with unossified lower limb; posttemporal fused to supracleithrum.

Vomer ossified, dentigerous; medial arm of maxilla twisted with no pronounced dorsal process; ventral arms gently curved toward and abutting rostral cartilage; outer arm narrow.

Premaxillary ascending processes flat and broad, tapered posteriorly and overlapping in the midline; rostral cartilage large and pentagonal; outer arm of premaxilla with alveolar process, not indented posteriorly. Ligament extending from ventral arms of maxillaries to middle of rostral cartilage; ethmomaxillary ligament present; meniscus present between premaxilla and maxilla.

Dentary not expanded medially, not robust; coronoid process on dentary overlapping with that of articular; retroarticular not elongate. Autopalatine with straight head, ventral process not elongate, not reaching quadrate; metapterygoid present.

Orbital rim free dorsally; anterior nares tubular; supraorbital sensory pores reduced to a series of neuromasts; seven preopercular pores, four mandibular pores; two or three lacrimal pores.

Males larger than females, often with fin extensions; pigment pattern in many cases composed of several dark crossbars on the sides of the body; all species with a spot at the anterior base of the dorsal fin at least in males; often a darkened caudal margin; middle rays of caudal elongate in juveniles and adults; throat bars present.

No fatty predorsal ridge; caudal scaled for one-third its length; swimbladder extending posteriorly to parhypural.

DISTRIBUTION: Indian subcontinent and Sri Lanka (Ceylon) eastward along the Indo-Malaysian Archipelago to Java.

REMARKS: Members of the genus *Aplocheilus* as defined herein have been most recently reviewed by Radda (1973). He followed Scheel (1972) in treating species of the genus *Epiplatys* as a subgenus, and therefore, referred to the species of *Aplocheilus* as forming a subgenus. In the present study *Aplocheilus* and *Epiplatys* are not considered to be synonyms, rather *Aplocheilus* is considered to be more closely related to the genus *Pachypanchax*.

Also, for a variety of reasons, *Aplocheilus* has long been considered to be the most primitive cyprinodontiform genus. Derived characters it shares with other Old World aplocheiloids refute this hypothesis.

MATERIAL EXAMINED: *A. panchax*: Gulf of Thailand, CAS 37934 (5*/64); India: Madras, SU 41523 (35); Malaya: SU 32785 (19). *A. lineatus*: India: Calicut: SU 41516 (3*/31). Aquarium material: AMNH 21498 SW (2+/2). *A. blocki*: S. India: Cochin: SU 41513 (14).

### GENUS *PACHYPANCHAX* MYERS

*Pachypanchax* Myers, 1933b, p. 1 (type species *Haplochilus playfairii* Günther, by original designation).

ETYMOLOGY: *Pachypanchax* from the Greek *pachy*, meaning robust and *Panchax*, a synonym of a related genus, referring to the robust appearance of this genus.

TYPES: Seychelles: *Haplochilus playfairii* Günther, Syntypes, BMNH 1864.11.15:91–93 (2).

COMPOSITION: Two species: *playfairi* (Günther), and *homalanotus* (Dumeril).

DIAGNOSIS: Distinguished from other cyprinodontiforms in having the posterior edge of scales of males angled away from the body in life; from other members of the *Aplocheilus-Pachypanchax-Epiplatys* group in having the hypural plates fused into a hypural fan in adults.

DEFINITION: Anal: ii, 15–ii, 16; Dorsal: ii, 9–iii, 9; Pelvic: 6; Pectoral: 19; Caudal: 6, 21, 6; Vertebrae: 13+16. Gill rakers on first arch: 10; Branchiostegal rays: 6. Scales lateral series: 25–27.

First pleural rib on parapophysis of second vertebra; parapophysis not reduced; no pleural ribs on hemal spines; hypural plates fused into hypural fan in adults, joint line visible in juveniles. Epipleural ribs not bifid.

Anal fin not modified into a gonopodium; anal fin musculature unmodified; first proximal radial present; middle anal radials present.

Spermatozeugmata not formed; fertilization external; development nonannual; oviparous. Eggs round.

One dorsal ray articulating with each of the first two dorsal radials; dorsal fin on posterior third of body.

Autopterotic fossa normal; lateral ethmoid not expanded medially, not reaching parasphenoid; parasphenoid not expanded anteriorly; weakly formed supraoccipital and epiotic processes; neural spine on first vertebra; first vertebra articulates with skull via basioccipital and exoccipital condyles; supraoccipital excluded from formation of foramen magnum; parietals present; nasals not expanded medially.

Mesethmoid cartilaginous; medial processes of pelvic fin base and ischial process reduced; interarcual cartilage large, attaches laterally to second pharyngobranchial which lacks bony flange; basihyal broad anteriorly, triangular ossification posteriorly; tooth patches on second and third hypobranchials; teeth on fourth ceratobranchials; dorsal and ventral hypohyal present; anterior extension of anterior ceratohyal ventral to hypohyals; no uncinate process on fourth epibranchial to articulate with that of third; first epibranchial narrow at its base. Interhyal ossified; three ossified basibranchials. Vomer with posterior extension dorsal to parasphenoid.

Lacrimal narrow and twisted carrying distinct sensory canal; dermosphenotic and preopercular with distinct sensory canal; pectoral girdle lowset; first postcleithrum present; posttemporal with unossified lower limb; posttemporal fused to supracleithrum.

Vomer ossified, dentigerous; medial arm of maxilla twisted with no pronounced dorsal process; ventral arms gently curved toward and abutting rostral cartilage; outer arm narrow.

Premaxillary ascending processes flat and broad, tapered posteriorly, not overlapping in the midline; rostral cartilage large and pentagonal; outer arm of premaxilla with alveolar process, not indented posteriorly. Ligament extending from ventral arms of maxillaries to middle of rostral cartilage; ethmomaxillary ligament present; meniscus present between premaxilla and maxilla.

Dentary not expanded medially, not robust; coronoid process on dentary overlapping with that of articular; retroarticular not elongate. Autopalatine with straight head, ventral process not elongate, not reaching quadrate; metapterygoid present.

Orbital rim free dorsally; anterior naris tubular; supraorbital sensory pores reduced to a series of neuromasts; seven preopercular pores, four mandibular pores; two or three lacrimal pores.

Males larger than females, never with fin extensions; pigment pattern not consisting of crossbars; males and females with faint red reticulations; juveniles and females with spot at anterior base of the dorsal fin (in *playfairi*); a darkened caudal and anal margin in males of *playfairi*; middle rays of caudal never elongate; throat bars present.

No fatty predorsal ridge; caudal scaled for at least one-third its length; swimbladder extending posteriorly to parhypural.

DISTRIBUTION: Madagascar, the Seychelles, coastal lowlands of eastern Mozambique, and Zanzibar north of the Zambezi River.

REMARKS: The genus *Pachypanchax* is considered to contain two species: *playfairi,* the type, and *homalanotus*. However, a specimen of *homalanotus* was not available for osteological examination, therefore, it is included with caution in the genus.

MATERIAL EXAMINED: *P. playfairi*: Seychelles: Syntypes as listed above, AMNH 20637 (4*/17); Zanzibar: AMNH 20701 (4*/19); Aquarium material: AMNH 38413 (3*/3); *P. homalanotus*: Aquarium material: SU 52679 (1).

## GENUS *EPIPLATYS* GILL

*Epiplatys* Gill, 1862, p. 136 (type species *Haplochilus sexfasciatus* Gill, by original designation).

ETYMOLOGY: *Epiplatys* from the Greek *epi,* meaning above, and *platys* meaning flat, referring to the flattened dorsal aspect of the skull.

TYPES: Gaboon: *Haplochilus sexfasciatus* Gill, Types, ANSP 7129 to 7141.

COMPOSITION: Over 50 nominal species and subspecies as listed in Lazara (1979).

DIAGNOSIS: Distinguished from other members of the *Aplocheilus-Pachypanchax-Epiplatys* group by the following primitive characters found derived in *Aplocheilus* and *Pachypanchax:* posttemporal with an ossified lower limb; orbital rim completely attached; no teeth on the hypobranchials; no darkened caudal margin, and no dorsal ocellus.

DEFINITION: Anal: iv, 12; Dorsal: iv, 7; Pelvic: 6; Pectoral: 17; Caudal: 6, 20, 6; Vertebrae: 11+14. Gill rakers on the anterior arm of the first arch: 8; Branchiostegal rays: 6. Scales lateral series: 26–30.

First pleural rib on parapophysis of second vertebra; parapophysis not reduced; a pleural rib often on first hemal spine; hypural plates divided, upper plate often divided in two. Epipleural ribs not bifid.

Anal fin not modified into a gonopodium; anal fin musculature unmodified; first proximal radial present; middle anal radials present.

Spermatozeugmata not formed; fertilization external; development nonannual; oviparous. Eggs round.

One dorsal ray articulating with each of the first two dorsal radials; dorsal fin on posterior third of body.

Autopterotic fossa normal; lateral ethmoid not expanded medially, not reaching parasphenoid; parasphenoid not expanded anteriorly; weakly formed supraoccipital and epiotic processes; neural spine on first vertebra; first vertebra articulates with skull via basioccipital and exoccipital condyles; supraoccipital excluded from formation of foramen magnum; parietals present; nasals not expanded medially.

Mesethmoid cartilaginous; medial processes of pelvic fin base and ischial process reduced; interarcual cartilage large, attaches laterally to second pharyngobranchial which lacks bony flange; basihyal broad anteriorly, triangular ossification posteriorly; no tooth patches on second and third hypobranchials; teeth on fourth ceratobranchials; dorsal and ventral hypohyal present; anterior extension of anterior ceratohyal ventral to hypohyals; no uncinate process on fourth epibranchial to articulate with that of third; first epibranchial narrow at its base. Interhyal ossified; three ossified basibranchials. Vomer with posterior extension dorsal to parasphenoid.

Lacrimal narrow and twisted carrying distinct sensory canal; dermosphenotic and preopercular with distinct sensory canal; pectoral girdle lowset; first postcleithrum present; posttemporal with ossified lower limb; posttemporal fused to supracleithrum.

Vomer ossified, dentigerous; medial arm of maxilla twisted with no pronounced dorsal process; ventral arms gently curved toward and abutting rostral cartilage; outer arm narrow.

Premaxillary ascending processes flat and broad, tapered posteriorly, not overlapping in the midline; rostral cartilage large and pentagonal; outer arm of premaxilla with alveolar process, not indented posteriorly. Ligament extending from ventral arms of maxillaries to middle of rostral cartilage; ethmomaxillary ligament present; meniscus present between premaxilla and maxilla.

Dentary not expanded medially, not robust; coronoid process on dentary not overlapping with that of articular; retroarticular not elongate. Autopalatine with straight head, ventral process not elongate, not reaching quadrate; metapterygoid present.

Orbital rim attached; anterior naris tubular; supraorbital sensory pores reduced to a series of neuromasts; seven preopercular pores, three mandibular pores; two or three lacrimal pores.

Males larger than females, often with fin extensions; pigment pattern often composed of several dark crossbars on the sides of the body; no species with a spot at the anterior base of the dorsal fin; middle rays of caudal elongate in juveniles and adults; throat bars present.

No fatty predorsal ridge; caudal scaled for at least one-third its length; swimbladder extending posteriorly to first or second hemal spine.

DISTRIBUTION: West and central Africa: eastward from Senegal, northern limit the Niger River, eastward to the Ethiopian Highlands, southward west of the Rift lakes to the Katanga Plateau, then eastward to the coast.

REMARKS: The genus *Epiplatys* as constituted in this study is paraphyletic. However, rather than create new generic names for subgroups of the genus which could not be incorporated into an overall phylogenetic scheme, the species group names which already exist are treated as subgenera of the genus *Epiplatys* until such time that they may be defined and their relationships determined. These subgenera are the following:

### SUBGENUS *LYCOCYPRINUS* PETERS

*Lycocyprinus* Peters, 1868, p. 146 (type species *Epiplatys dageti* Poll by monotypy).

### SUBGENUS *PAREPIPLATYS* CLAUSEN

*Parepiplatys* Clausen, 1967, p. 28 (type species *Haplochilus grahami* Boulenger, by original designation [proposed as a subgenus]).

### SUBGENUS *PSEUDEPIPLATYS* CLAUSEN

*Pseudepiplatys* Clausen, 1967, p. 30 (type species *Haplochilus annulatus* Boulenger, by original designation [proposed as a subgenus]).

### SUBGENUS *APHYOPLATYS* CLAUSEN

*Aphyoplatys* Clausen, 1967, p. 32 (type species *Epiplatys duboisi* Poll, by original designation [proposed as a subgenus]).

MATERIAL EXAMINED: *E. sexfasciatus*: Dahomey, Iquidi R: USNM 218752 (2*/21); *E. chaperi*: Ghana: SU 64709 (1*/12); *E. fasciolatus*: Liberia: Tchien: AMNH 32735 (5*/10); *E. bifasciatus*: Nigeria (Aquarium material) AMNH 21866SW (1+/1). *E. senegalensis*: Nigeria (Aquarium material) AMNH 21867 (1+/1); *E. dageti*: Ghana: SU 64640 (29). *Haplochilus annulatus*: Type: Sierra Leone: BMNH 1914. 12. 9: 5–6.

### GENUS *APHYOSEMION* MYERS

*Aphyosemion* Myers, 1924b, p. 2 (type species *Aphysemion castaneum* Myers, by original designation).

ETYMOLOGY: *Aphyosemion* from the Greek *aphyos*, meaning small and *semion* meaning flag or banner referring to the lyre-shaped caudal fin of males.

TYPES: Zaire (Congo): *Aphyosemion castaneum* Myers, Type AMNH 8337 (1).

COMPOSITION: Approximately 60 species as listed in Lazara (1979).

DIAGNOSIS: Distinguished from other members of the *Aphyosemion-Nothobranchius* group by being nonannual, having a dorsal fin of seven to 14 rays which is situated no farther anteriorly than opposite the first quarter of the anal fin orgin, and possessing a swimbladder extending posteriorly to the first one or two hemal spines.

DEFINITION: Anal: iii, 12; Dorsal: i, 6–ii, 12; Pelvic: 6; Pectoral: 16–17; Caudal: 8, 13, 8; Vertebrae: 13+15. Gill rakers on anterior arm of the first arch: 8, 9; Branchiostegal rays: 6. Scales Lateral Series: 29–33.

First pleural rib on parapophysis of second vertebra; parapophysis not reduced; no pleural rib on first hemal spine; hypural plates divided, upper plate never divided in two. Epipleural ribs bifid.

Anal fin not modified into a gonopodium; anal fin musculature unmodified; first proximal radial present; middle anal radials present.

Spermatozeugmata not formed; fertilization external; development nonannual; oviparous. Eggs round.

One dorsal ray articulating with each of the first two dorsal radials; dorsal fin on posterior third of body.

Autopterotic fossa normal; lateral ethmoid not expanded medially, not reaching parasphenoid; parasphenoid not expanded anteriorly; weakly formed supraoccipital and epiotic processes; neural spine on first vertebra; first vertebra articulates with skull via basioccipital and exoccipital condyles; supraoccipital excluded from formation of foramen magnum; parietals present; nasals not expanded medially.

Mesethmoid cartilaginous; medial processes of pelvic fin base and ischial process reduced; interarcual cartilage large, attaches laterally to second pharyngobranchial which lacks bony flange; basihyal broad anteriorly, triangular ossification posteriorly; no tooth patches on second and third hypobranchials; teeth on fourth ceratobranchials; dorsal and ventral hypohyal present; anterior extension of anterior ceratohyal ventral to hypohyals; uncinate process on fourth epibranchial articulates with that of third; first epibranchial narrow at its base. Interhyal ossified; three ossified basibranchials. Vomer with attenuate posterior extension dorsal to parasphenoid.

Lacrimal narrow and twisted carrying distinct sensory canal; dermosphenotic and preopercular with distinct sensory canal; pectoral girdle lowset; first postcleithrum present; posttemporal with ossified lower limb; posttemporal fused to supracleithrum.

Vomer ossified, dentigerous; medial arm of maxilla twisted with no pronounced dorsal process; ventral arms gently curved toward and abutting rostral cartilage; outer arm narrow.

Premaxillary ascending processes flat and broad, tapered posteriorly not overlapping in the midline; rostral cartilage large and pentagonal; outer arm of premaxilla with alveolar process, not indented posteriorly. Ligament extending from ventral arms of maxillaries to middle of rostral cartilage; ethmomaxillary ligament present; meniscus present between premaxilla and maxilla.

Dentary not expanded medially, not robust; coronoid process on dentary not overlapping with that of articular; retroarticular not elongate. Autopalatine with straight head, ventral process not elongate, not reaching quadrate; metapterygoid present.

Orbital rim attached; anterior naris tubular; supraorbital sensory pores reduced to a series of neuromasts; seven preopercular pores, four mandibular pores; two or three lacrimal pores.

Males larger than females, often with fin extensions; pigment pattern rarely composed of several dark crossbars on the sides of the body; no species with a spot at the anterior base of the dorsal fin; rarely middle rays of caudal elongate in juveniles and adults; throat bars weakly present. Males with light dorsal and ventral caudal margins; often light anal caudal margins; "wound" spot typically present.

No fatty predorsal ridge; caudal scaled for at least one-third its length; swimbladder extending posteriorly to first one or two hemal spines.

DISTRIBUTION: Western central Africa, concentrated in the Congo Basin, westward to Gambia along the coast.

REMARKS: *Aphyosemion* Myers cannot be defined as a monophyletic group; nor are the interrelationships of its named subgenera within the scope of the present paper. Most supraspecific categories are recently named and encompass a large number of species. Therefore, the genus *Aphyosemion* is divided into two major groupings, one encompassing the more primitive species and the other encompassing the more derived species that are more closely related to *Nothobranchius* than to other species of *Aphyosemion*. The primitive members are referred to the genus *Aphyosemion,* whereas the derived members are referred to the genus *Fundulopanchax,* an available supraspecific category. Huber (1978) grouped all the subgenera within *Aphyosemion,* therefore not recognizing the closer association of *Fundulopanchax* to *Nothobranchius*. The subgenera of *Aphyosemion* of the more primitive grouping are:

### SUBGENUS *ARCHIAPHYOSEMION* RADDA

*Archiaphyosemion* Radda, 1977, p. 214 (type species *Aphyosemion guineense* Daget, by original designation [proposed as a subgenus]).

### SUBGENUS *CHROMAPHYOSEMION* RADDA

*Chromaphyosemion* Radda, 1971, p. 157 (type species *Fundulus bivittatus* Boulenger, by original designation [proposed as a subgenus]).

### SUBGENUS *DIAPTERON* HUBER AND SEEGERS

*Diapteron* Huber and Seegers, 1977, p. 146 (type species *Aphyosemion georgiae* Lambert and Gery by original designation [proposed as a subgenus]).

### SUBGENUS *KATHETYS* HUBER

*Kathetys* Huber, 1977, p. 8 (type species *Fundulus exiguus* Boulenger by original designation [proposed as a subgenus]).

### SUBGENUS *MESOAPHYOSEMION* RADDA

*Mesoaphyosemion* Radda, 1977, p. 213 (type species *Haplochilus cameronensis* Boulenger, by original designation [proposed as a subgenus]).

MATERIAL EXAMINED: *A. castaneum*: Zaire: type as listed above; Paratypes: AMNH 8338 (1*/4); *A. petersi*: Aquarium material AMNH 21572 (2+/2); Ghana: SU 64709 (2*/28). *A. cameronensis*: Cameroon: Ntem R. SU 15713 (8). *A. bivittatum*: Cameroon: SU55491 (1*/6).

## GENUS *FUNDULOPANCHAX* MYERS

*Fundulopanchax* Myers, 1924b, p. 4 (type species *Fundulus sjoestedti* Lonnberg, by monotypy [proposed as a subgenus]).

ETYMOLOGY: *Fundulopanchax* from *Fundulus* and *Panchax,* two nominal genera, the former from the New World and the latter from the Old World, between which *Fundulopanchax* was thought to be intermediate.

COMPOSITION: Approximately 50 species currently referred to the included subgeneric categories.

DIAGNOSIS: Distinguished from other species of *Aphyosemion* by elongate dorsal fin of 14 rays or more, and the swimbladder which does not penetrate beyond the first hemal spine. All included species are annual.

DEFINITION: Anal: iii, 13; Dorsal: i, 13–ii, 18; Pelvic: 6; Pectoral: 17–18; Caudal: 8, 14, 8; Vertebrae: 12+15–14+19. Gill rakers on anterior arm of the first arch: 12, Branchiostegal rays: 6; Scales lateral series: 33–37.

First pleural rib on parapophysis of second vertebra; parapophysis not reduced; no pleural rib on first hemal spine; hypural plates divided, upper plate never divided in two. Epipleural ribs bifid.

Anal fin not modified into a gonopodium;

anal fin musculature unmodified; first proximal radial present; middle anal radials present.

Spermatozeugmata not formed; fertilization external; development annual; oviparous. Eggs round.

One dorsal ray articulating with each of the first two dorsal radials; dorsal fin opposite or anterior to origin of anal.

Autopterotic fossa normal; lateral ethmoid not expanded medially, not reaching parasphenoid; parasphenoid not expanded anteriorly; weakly formed supraoccipital and epiotic processes; neural spine on first vertebra; first vertebra articulates with skull via basioccipital and exoccipital condyles; supraoccipital excluded from formation of foramen magnum; parietals present; nasals not expanded medially.

Mesethmoid cartilaginous; medial processes of pelvic fin base and ischial process reduced; interarcual cartilage large, attaches laterally to second pharyngobranchial which lacks bony flange; basihyal broad anteriorly, triangular ossification posteriorly; no tooth patches on second and third hypobranchials; teeth on fourth ceratobranchials; dorsal and ventral hypohyal present; anterior extension of anterior ceratohyal ventral to hypohyals; uncinate process on fourth epibranchial articulates with that of third; first epibranchial narrow at its base. Interhyal ossified; three ossified basibranchials. Vomer with attenuate posterior extension dorsal to parasphenoid.

Lacrimal narrow and twisted carrying distinct sensory canal; dermosphenotic and preopercular with distinct sensory canal; pectoral girdle lowset; first postcleithrum present; posttemporal with ossified lower limb; posttemporal fused to supracleithrum.

Vomer ossified, dentigerous; medial arm of maxilla twisted with no pronounced dorsal process; ventral arms gently curved toward and abutting rostral cartilage; outer arm narrow.

Premaxillary ascending processes flat and broad, tapered posteriorly not overlapping in the midline; rostral cartilage large and pentagonal; outer arm of premaxilla with alveolar process, not indented posteriorly. Ligament extending from ventral arms of maxillaries to middle of rostral cartilage; ethmomaxillary ligament present; meniscus present between premaxilla and maxilla.

Dentary not expanded medially, not robust; coronoid process on dentary not overlapping with that of articular; retroarticular not elongate. Autopalatine with straight head, ventral process not elongate, not reaching quadrate; metapterygoid present.

Orbital rim attached; anterior naris tubular; supraorbital sensory pores reduced to a series of neuromasts; seven preopercular pores, four mandibular pores; two or three lacrimal pores.

Males larger than females, often with fin extensions; pigment pattern rarely composed of several dark crossbars on the sides of the body; no species with a spot at the anterior base of the dorsal fin; often middle rays of caudal elongate in juveniles and adults; "Wound" mark typically present; males often with light dorsal and ventral margins of caudal, as well as dorsal and anal.

No fatty predorsal ridge; caudal scaled for at least one third its length; swimbladder extending just to the first hemal spine.

DISTRIBUTION: Congo Basin.

REMARKS: *Fundulopanchax* contains species previously assigned to *Aphyosemion* that are more closely related to *Nothobranchius* than to the more primitive species of *Aphyosemion*. This usage of the genus *Fundulopanchax* differs from that of Loiselle and Glasgow (1971) who limited the group to large forms such as *sjoestedti*.

The designation of a type species for the genus *Callopanchax* as *A. occidentale* by the International Commission places the genus *Roloffia* as an objective synonym of *Callopanchax*. This decision has been rejected by many aquarists who believe that Myers (1924b) had either *sjoestedti* or another species in hand when he named the subgenus *Callopanchax*, with *sjoestedti* as the type, even though giving a description of *occidentale*. It is interesting to note that the sole lot catalogued as *sjoestedti* in the collection of the AMNH is an aquarium lot of *occiden-*

*tale*. Therefore, it is likely that Myers had specimens of *occidentale* not *sjoestedti* in hand when naming *Callopanchax*.

The subgenera placed in *Fundulopanchax* are:

### SUBGENUS *PALUDOPANCHAX* RADDA

*Paludopanchax* Radda, 1977, p. 211 (type species *Fundulus arnoldi* Boulenger, by original designation).

### SUBGENUS *PARAPHYOSEMION* KOTTELAT

*Paraphyosemion* Kottelat, 1976, p. 158 (type species *Fundulus gardneri* Boulenger, by original designation [proposed as a subgenus]).

### SUBGENUS *GULAROPANCHAX* RADDA

*Gularopanchax* Radda, 1977, p. 210 (type species *Fundulus gularis* Boulenger, by original designation [proposed as a subgenus]).

### SUBGENUS *CALLOPANCHAX* MYERS

*Callopanchax* Myers, 1933c, p. 184 (type species *Aphyosemion occidentale* Roloff, by monotypy [proposed as a subgenus]).

*Roloffia* Clausen, 1966, p. 388 (type species *Aphyosemion occidentale* Roloff, by original designation).

### SUBGENUS *RADDAELLA* HUBER

*Raddaella* Huber, 1977, p. 8 (type species *Fundulus batesi* Boulenger, by original designation [proposed as a subgenus]).

MATERIAL EXAMINED: *F. sjoestedti*: Aquarium material: AMNH 21575 (4+/4); *F. gardneri*: Ghana: SU 64693 (1*/7); *F. gulare*: Aquarium material: AMNH 20563 (3+/13); *F. arnoldi*: Nigeria: Port Harcourt: AMNH 21570 (1+/1). *F. occidentale*: Aquarium material: AMNH 14611 (2*/6).

## GENUS *ADAMAS* HUBER

*Adamas* Huber, 1979, p. 5, 6 (type species *Adamas formosus* Huber, by original designation).

ETYMOLOGY: *Adamas* from the Greek, meaning steel or diamond which refers to the brilliant frontal spot.

TYPES: Zaire: Village of Ntokon near the banks of the Likouala-Mossaka. *Adamas formosus* Huber, Holotype MNHN 1979-199 (1).

COMPOSITION: Solely the type species.

DIAGNOSIS: Distinguished from other aplocheiloids by the presence of a brilliant diamond shaped frontal spot.

DEFINITION: Anal: 15, Dorsal: 8–9; dorsal fin originates opposite the twelfth to fourteenth rays of anal.

Both males and females are characterized by a brilliant diamond-shaped frontal spot. There are no dark crossbars.

DISTRIBUTION: That of the type locality and environs.

REMARKS: Specimens of this new genus and species have not been examined. Data are from the original description of Huber (1979).

Huber considered it difficult to place his new genus in a subfamily of aplocheiloids or of procatopines, citing as evidence of relationship with the former the overall morphology and color pattern, and with the latter the behavior and biology, on which he did not elaborate.

On the basis of its external morphology and dorsal and anal fin ray number and position, I consider *Adamas* to represent just one more species allied to *Aphyosemion*. The concept that the Old World aplocheiloids and procatopines are closely related has prevailed, although there is no evidence to support such a relationship.

## GENUS *NOTHOBRANCHIUS* PETERS

*Nothobranchius* Peters, 1868, p. 10 (type species *Cyprinodon orthonotus* Peters, by original designation).

*Adiniops* Myers, 1924b, p. 6 (type species *Fundulus guentheri* Pfeffer, by original designation [proposed as a subgenus]).

*Fundulosoma* Ahl, 1924, p. 52 (type species *Fundulosoma thierryi* Ahl, by original designation).

*Pronothobranchius* Radda, 1969, p. 4 (type species *Nothobranchius kiyawensis* Ahl, by original designation [proposed as a subgenus]).

*Zonothobranchius* Radda, 1969, p. 4 (type species *Nothobranchius rubroreticulatus* Blache and

Miton, by original designation [proposed as a subgenus]).

*Aphyobranchius* Wildekamp, 1977, p. 327 (type species *Nothobranchius janpapi* Wildekamp, by original designation [proposed as a subgenus]).

ETYMOLOGY: *Nothobranchius*, from the Greek *nothos*, meaning false and *branchia* meaning gills, in reference to the restricted gill opening.

TYPES: Mozambique: Quelimane: *Cyprinodon orthonotus* Peters, Syntype BMNH 1861. 5.2: 88-9 (1).

COMPOSITION: Approximately 35 species as listed in Lazara (1979).

DIAGNOSIS: Distinguished from all other cyprinodontiforms by the interarcual cartilage attaching directly to the cartilage of the second pharyngobranchial and oval, rather than round eggs; and from other aplocheiloids by an uncovered preopercular canal.

DEFINITION: Anal: ii, 13–ii, 17; Dorsal: ii, 13–ii, 16; pelvic: 6; Pectoral: 16–21; Caudal: 8, 15, 8; Vertebrae: 12+15–12+17. Gill rakers on anterior arm of the first arch: 12–21. Branchiostegal rays: 6–7; Scales lateral series: 26–42.

First pleural rib on parapophysis of second vertebra; parapophysis not reduced; no pleural rib on first hemal spine; hypural plates fused into a hypural fan. Epipleural ribs bifid.

Anal fin not modified into a gonopodium; anal fin musculature unmodified; first proximal radial present; middle anal radials present.

Spermatozeugmata not formed; fertilization external; development annual; oviparous. Eggs oval.

One dorsal ray articulating with each of the first two dorsal radials; dorsal fin opposite or anterior to origin of anal.

Autopterotic fossa normal; lateral ethmoid not expanded medially, not reaching parasphenoid; parasphenoid not expanded anteriorly; weakly formed supraoccipital and epiotic processes; neural spine on first vertebra; first vertebra articulates with skull via basioccipital and exoccipital condyles; supraoccipital excluded from formation of foramen magnum; parietals present; nasals not expanded medially.

Mesethmoid cartilaginous; medial processes of pelvic fin base and ischial process reduced; interarcual cartilage large, attaches directly to articulation point, second pharyngobranchial which lacks bony flange; basihyal broad anteriorly, triangular ossification posteriorly; no tooth patches on second and third hypobranchials; teeth on fourth ceratobranchials; dorsal and ventral hypohyal present; anterior extension of anterior ceratohyal ventral to hypohyals; uncinate process on fourth epibranchial articulates with that of third; first epibranchial narrow at its base. Interhyal ossified; three ossified basibranchials. Vomer with attenuate posterior extension dorsal to parasphenoid.

Lacrimal narrow and twisted carrying distinct sensory canal; dermosphenotic and preopercular with distinct sensory canal; pectoral girdle lowset; first postcleithrum present; posttemporal with ossified lower limb; posttemporal fused to supracleithrum.

Vomer ossified, dentigerous; medial arm of maxilla twisted with no pronounced dorsal process; ventral arms gently curved toward and abutting rostral cartilage; outer arm narrow.

Premaxillary ascending processes flat and broad, tapered posteriorly not overlapping in the midline; rostral cartilage large and pentagonal; outer arm of premaxilla with alveolar process, not indented posteriorly. Ligament extending from ventral arms of maxillaries to middle of rostral cartilage; ethmomaxillary ligament present; meniscus present between premaxilla and maxilla.

Dentary not expanded medially, not robust; coronoid process on dentary not overlapping with that of articular; retroarticular not elongate. Autopalatine with straight head, ventral process not elongate, not reaching quadrate; metapterygoid present.

Orbital rim attached; anterior nares tubular; supraorbital sensory pores reduced to a series of neuromasts; preopercular canal represented by an open groove, four mandibular pores; two or three lacrimal pores.

Males larger than females, caudal fin extension in *thierryi*; caudal typically rounded; pigmentation pattern typically consisting of red reticulations, or body uniformly red and blue throughout. Vertical bar through eye in one species (*microlepis*).

No fatty predorsal ridge; caudal scaled for at least one third its length; swimbladder extending to the first hemal spine.

DISTRIBUTION: West central and east Africa, northern limit the Niger River, east to Somalia, and south to northern South Africa.

REMARKS: The composition of the genus *Nothobranchius* is increased here by one species, *thierryi*, formally placed in the monotypic *Fundulosoma*. There is no representative of this genus in the Seychelles, and the description of *N. seychellensis* seems to have been based on material from Africa.

MATERIAL EXAMINED: *N. orthonotus*: Mozambique: the type as listed above; Kruger National Park: AMNH 22255SW (1+/1). *N. thierryi*: Ghana: BMNH 1970.10.22.1–13. (1*/6); *N. guentheri*: Zanzibar: AMNH 22252 (19+/19); *N. melanospilus*: Aquarium material: USNM uncat. (1*/8); *N. kirki*: Aquarium material: AMNH 38407 (2*/2); *N. microlepis*: Somalia Meridonele: MCSN 15163 (4) Syntypes, AMNH 20588 (1*/4), Syntypes; *N. patrizii*: Somalia: MCSN 33702 (4) Syntypes, AMNH 20587 (4) Syntypes; *N. kiyawensis*: Nigeria: Cotypes USNM 92820 (2).

## FAMILY RIVULIDAE MYERS

Type Genus *Rivulus* Poey, 1860.

DIAGNOSIS: The Rivulidae differ from all other aplocheiloids by lacking the first postcleithrum and from other cyprinodontiforms by having a preoperculum and lacrimal with obsolescent sensory canals, lateral ethmoid expanded medially under the lateral extension of the vomer, opercular, and branchiostegal membranes united and often covered with scales, urohyal not distinct externally, a unique headscale pattern, and a triangular flange on the anterior face of the ventral process of the maxilla.

COMPOSITION: Nine genera: *Rivulus*, "*Rivulus*," *Trigonectes*, *Neofundulus*, "*Neofundulus*," *Rachovia*, *Cynolebias*, *Pterolebias* and *Austrofundulus*.

DISTRIBUTION: (fig. 18) New World from southern Florida and the Bahamas, Cuba, Hispaniola, Trinidad, Middle America, south through South America to Uruguay.

## GENUS *RIVULUS* POEY

*Rivulus* Poey, 1860, p. 307 (type species *Rivulus cylindraceus* Poey, by original designation).

*Cynodonichthys* Meek, 1904, p. 101 (type species *Cynodonichthys tenuis* Meek, by original designation).

*Vomerivulus* Fowler, 1944, p. 244 (type species *Rivulus leucurus* Fowler, by original designation).

ETYMOLOGY: The genus *Rivulus* meaning small stream or rivulet, the typical habitat of these killifishes.

TYPES: Cuba: Stream at Mardaza, near Havana: *Rivulus cylindraceus* Poey. Types MCZ 6397 (3).

COMPOSITION: Smaller nonannual species presently referred to *Rivulus* (as in Lazara, 1979) including *cylindraceus*, *heyei*, and *marmoratus*.

DIAGNOSIS: Neotropical aplocheiloids with ossified interhyals, fin rays not elongate and six pelvic fin rays.

DEFINITION: Anal: ii, 9–ii, 12; Dorsal: i, 8; Pelvic: 6; Pectoral: 13–14; Caudal: 8, 14, 8–8, 18, 8; Vertebrae: 14+16–20+20. Gill rakers on anterior arm of the first arch: 8; Branchiostegal rays: 6. Scales lateral series: 34–51.

First pleural rib on parapophysis of second vertebra; parapophysis not reduced; no pleural rib on first hemal spine; hypural plates divided, upper plate never divided in two. Epipleural ribs not bifid.

Anal fin not modified into a gonopodium; anal fin musculature unmodified; first proximal radial present; middle anal radials present.

Spermatozeugmata not formed; fertilization external; development nonannual; oviparous. Eggs round.

One dorsal ray articulating with each of the first two dorsal radials; dorsal fin on posterior third of body.

Autopterotic fossa normal; lateral ethmoid expanded medially, extending under parasphenoid; parasphenoid slightly expanded anteriorly; weakly formed supraoccipital and epiotic processes; neural spine on first vertebra; first vertebra articulates with skull via basioccipital and exoccipital condyles; supraoccipital excluded from formation of foramen magnum; parietals present; nasals not expanded medially.

Mesethmoid cartilaginous; medial processes of pelvic fin base and ischial process reduced; interarcual cartilage large, attaches laterally to second pharyngobranchial which possesses a bony flange; basihyal broad anteriorly, elongate ossification posteriorly; no tooth patches on second and third hypobranchials; teeth on fourth ceratobranchials; dorsal and ventral hypohyal present; anterior extension of anterior ceratohyal ventral to hypohyals; uncinate process on fourth epibranchial articulates with that of third; first epibranchial narrow at its base. Interhyal ossified; three ossified basibranchials. Vomer with posterior extension dorsal to parasphenoid.

Lacrimal narrow and twisted with obsolescent sensory canal; dermosphenotic and preopercular with obsolescent sensory canal; pectoral girdle lowset; first postcleithrum absent; posttemporal with ossified lower limb; posttemporal not fused to supracleithrum.

Vomer ossified, dentigerous; medial arm of maxilla twisted with no pronounced dorsal process; ventral arms with pronounced anterior extension abutting rostral cartilage; outer arm narrow.

Premaxillary ascending processes flat and broad, not tapered posteriorly not overlapping in the midline; rostral cartilage large and pentagonal; outer arm of premaxilla with alveolar process, not indented posteriorly. Ligament extending from ventral arms of maxillaries to middle of rostral cartilage; ethmomaxillary ligament present; meniscus present between premaxilla and maxilla.

Dentary not expanded medially, not robust; coronoid process on dentary not overlapping with that of articular; retroarticular not elongate. Autopalatine with straight head, ventral process not elongate, not reaching quadrate; metapterygoid present.

Orbital rim attached; anterior nares tubular; supraorbital sensory pores reduced to a series of neuromasts; preopercular, mandibular, and lacrimal pores absent, replaced by a series of weakly formed neuromasts. Branchiostegal rays covered.

Males larger than females, all fins rounded; females with distinct caudal ocellus; males with light dorsal and ventral caudal fin margins; no species with a spot at the anterior base of the dorsal fin; middle rays of caudal never elongate in juveniles and adults; throat bars weakly present.

No fatty predorsal ridge; caudal scaled for at least one-third its length; swimbladder extending posteriorly to first one or two hemal spines.

DISTRIBUTION: *Rivulus* and "*Rivulus*" have distribution patterns nearly coincident with that of the family, as listed above. "*Rivulus*" is excluded from North America, however.

REMARKS: *Rivulus* as constituted traditionally is not monophyletic. Species assigned to the genus may be divided into two groups, one a primitive assemblage of species which possess an ossified interhyal, six pelvic fin rays, and dorsal and anal fin rays that are not elongate. These species, which include the type *cylindraceus* and other diminutive forms (including *marmoratus* and *heyei*), are referred to the genus *Rivulus*. The other group of species, of which *harti* may be considered representative, have a cartilaginous interhyal, seven pelvic fin rays and elongate dorsal and anal fin rays, derived characters they share with Neotropical aplocheiloids. These species are referred to the genus "*Rivulus*" until they are revised at the species level, and monophyletic groups of species recognized within both assemblages.

Hoedeman (1961) presented a key to the recognized species and subspecies of the genus *Rivulus* (which includes the genera *Rivulus* and "*Rivulus*" herein).

MATERIAL EXAMINED: Cuba: *R. cylindra-*

*ceus*: the types as listed above; SU 32018 (2); *R. marmoratus*: Cuba: USNM 164438 (1*/6); Florida: AMNH 16117 (6). *R. tenuis*: Guatemala: Alta Verapaz: AMNH 32069 (2+/2).

### GENUS "*RIVULUS*"

ETYMOLOGY: "*Rivulus*" is used to reference the more derived species of the genus *Rivulus*.

DIAGNOSIS: Neotropical aplocheiloids with an ossified interhyal, elongate pelvic fin rays, seven or eight pelvic fin rays and known or inferred annual habit, characters which they share with the more derived genera of the group.

DEFINITION: Anal: iii, 12; Dorsal: i, 8; Pelvic: 7–8; Pectoral: 16; Caudal: 8, 15, 8; Vertebrae: 12+18. Gill rakers on anterior arm of the first arch: 8, 9; Branchiostegal rays: 6; Scales lateral series: 35–36.

First pleural rib on parapophysis of second vertebra; parapophysis not reduced; no pleural rib on first hemal spine; hypural plates divided, upper plate never divided in two. Epipleural ribs not bifid.

Anal fin not modified into a gonopodium; anal fin musculature unmodified; first proximal radial present; middle anal radials present.

Spermatozeugmata not formed; fertilization external; development known to be annual in at least one species; oviparous. Eggs round.

One dorsal ray articulating with each of the first two dorsal radials; dorsal fin on posterior third of body.

Autopterotic fossa normal; lateral ethmoid expanded medially, extending under parasphenoid; parasphenoid slightly expanded anteriorly; weakly formed supraoccipital and epiotic processes; neural spine on first vertebra; first vertebra articulates with skull via basioccipital and exoccipital condyles; supraoccipital excluded from formation of foramen magnum; parietals present; nasals not expanded medially.

Mesethmoid cartilaginous; medial processes of pelvic fin base and ischial process reduced; interarcual cartilage large, attaches laterally to second pharyngobranchial which possesses a bony flange; basihyal broad anteriorly, elongate ossification posteriorly; no tooth patches on second and third hypobranchials; teeth on fourth ceratobranchials; dorsal and ventral hypohyal present; anterior extension of anterior ceratohyal ventral to hypohyals; uncinate process on fourth epibranchial articulates with that of third; first epibranchial narrow at its base. Interhyal cartilaginous; three ossified basibranchials. Vomer with posterior extension dorsal to parasphenoid.

Lacrimal narrow and twisted with obsolescent sensory canal; dermosphenotic and preopercular with obsolescent sensory canal; pectoral girdle lowset; first postcleithrum absent; posttemporal with ossified lower limb; posttemporal not fused to supracleithrum.

Vomer ossified, dentigerous; medial arm of maxilla twisted with no pronounced dorsal process; ventral arms with pronounced anterior extension abutting rostral cartilage; outer arm narrow.

Premaxillary ascending processes flat and broad, not tapered posteriorly, not overlapping in the midline; rostral cartilage enlarged and rectangular; outer arm of premaxilla with alveolar process, not indented posteriorly. Ligament extending from ventral arms of maxillaries to middle of rostral cartilage; ethmomaxillary ligament present; meniscus present between premaxilla and maxilla.

Dentary not expanded medially, not robust; coronoid process on dentary not overlapping with that of articular; retroarticular not elongate. Autopalatine with straight head, ventral process not elongate, not reaching quadrate; metapterygoid present.

Orbital rim attached; anterior nares tubular; supraorbital sensory pores reduced to a series of neuromasts; preopercular, mandibular and lacrimal pores absent, replaced by a series of weakly formed neuromasts. Branchiostegal rays covered.

Males larger than females, often with fin extensions; females with distinct caudal ocellus; males with light dorsal and ventral caudal fin margins; no species with a spot at the anterior base of the dorsal fin; middle rays of caudal never elongate in juveniles and adults; throat bars weakly present.

No fatty predorsal ridge; caudal scaled for at least one-third its length; swimbladder extending posteriorly to first one or two hemal spines.

DISTRIBUTION: See *Rivulus* above.

REMARKS: In the description of the annual *Rivulus stellifer* Thomerson and Turner (1973) stated that they believed it served as a link between the nonannual forms and the annual Neotropical aplocheiloids. Their suggestion has been supported here; however, the position of *stellifer* is restated as more closely related to the annual genera than it is to the nonannual species of *Rivulus*.

MATERIAL EXAMINED: *R. harti*: Trinidad: AMNH 15189 (2*/19); Venezuela: Margarita Is.: AMNH 8354 (2+/2). *R. stellifer*: Venezuela: Cojedes: Paratopotypes: CAS 27556 (2).

### GENUS *TRIGONECTES* MYERS

*Trigonectes* Myers, 1925, p. 371 (type species *Trigonectes strigabundus* Myers, by original designation).

*Rivulichthys* Myers, 1927, p. 118 (type species *Rivulus rondoni* Ribeiro, by original designation).

ETYMOLOGY: *Trigonectes* from the Greek *trig*, meaning angular and *nektos*, to swim, referring to the wedge-shaped schools in which members have been observed.

TYPES: Brazil: Goias: Porto Nacional, Donna Francisquinha into Tocantins. *Trigonectes strigabundus* Myers, Holotype CAS 40701 (1).

COMPOSITION: Four species: *strigabundus* Myers, *rondoni* (Myers), *rogaoguae* (Pearson and Myers), and *luelingi* (Meinken).

DIAGNOSIS: Distinguished from all other cyprinodontiforms by an oblique mouth cleft caused by a reduction in the anterior ramus of the alveolar arm of the premaxilla.

DEFINITION: Anal: ii, 15; Dorsal: ii, 9; Pelvic: 7; Pectoral: 13–14; Caudal: 6, 16, 6; Vertebrae: 13+15. Gill rakers on anterior arm of the first arch: 11. Branchiostegal rays: 6. Scales lateral series: 35–41.

First pleural rib on parapophysis of second vertebra; parapophysis not reduced; no pleural rib on first hemal spine; hypural plates divided, upper plate never divided in two. Epipleural ribs not bifid.

Anal fin not modified into a gonopodium; anal fin musculature unmodified; first proximal radial present; middle anal radials present.

Spermatozeugmata not formed; fertilization external; development inferred to be annual; oviparous. Eggs round.

One dorsal ray articulating with each of the first two dorsal radials; dorsal fin on posterior third of body.

Autopterotic fossa normal; lateral ethmoid expanded medially, extending under parasphenoid; parasphenoid slightly expanded anteriorly; weakly formed supraoccipital and epiotic processes; neural spine on first vertebra; first vertebra articulates with skull via basioccipital and exoccipital condyles; supraoccipital excluded from formation of foramen magnum; parietals present; nasals not expanded medially.

Mesethmoid cartilaginous; medial processes of pelvic fin base and ischial process reduced; interarcual cartilage large, attaches laterally to second pharyngobranchial which possesses a bony flange; basihyal broad anteriorly, elongate ossification posteriorly; no tooth patches on second and third hypobranchials; teeth on fourth ceratobranchials; dorsal and ventral hypohyal present; anterior extension of anterior ceratohyal ventral to hypohyals; uncinate process on fourth epibranchial articulates with that of third; first epibranchial narrow at its base. Interhyal cartilaginous; three ossified basibranchials. Vomer with posterior extension dorsal to parasphenoid.

Lacrimal narrow and twisted with obsolescent sensory canal; dermosphenotic and preopercular with obsolescent sensory canal; pectoral girdle lowset; first postcleithrum absent; posttemporal with ossified lower limb; posttemporal not fused to supracleithrum.

Vomer ossified, dentigerous; medial arm of maxilla twisted with no pronounced dorsal process; ventral arms with pronounced anterior extension abutting rostral cartilage; outer arm narrow.

Premaxillary ascending processes flat and broad, not tapered posteriorly not overlapping in the midline; rostral cartilage enlarged and rectangular; outer arm of premaxilla with alveolar process, not indented posteriorly, anterior ramus reduced; mouth cleft oblique. Ligament extending from ventral arms of maxillaries to middle of rostral cartilage; ethmomaxillary ligament present; meniscus present between premaxilla and maxilla.

Dentary not expanded medially, not robust; coronoid process on dentary not overlapping with that of articular; retroarticular not elongate. Autopalatine with straight head, ventral process not elongate, not reaching quadrate; metapterygoid present.

Orbital rim attached; anterior naris tubular; supraorbital sensory pores reduced to a series of neuromasts preopercular, mandibular and lacrimal pores absent, replaced by a series of weakly formed neuromasts. Branchiostegal rays covered.

Males larger than females, often with fin extensions; pigmentation pattern consisting of even rows of brown or reddish brown reticulations along the side of the body, and extending onto the unpaired fins.

No fatty predorsal ridge; caudal scaled for at least one-third its length; swimbladder extending posteriorly to first one or two hemal spines.

DISTRIBUTION: Paraguay; Brazil; Bolivia (Lake Rogoaga).

REMARKS: *Trigonectes strigabundus* is represented in collections only by the holotype and four paratypes.

MATERIAL EXAMINED: *T. strigabundus*: the types as listed above; Paratypes: CAS 40702 (1* gill arches only/4); *T. rondoni*: Paraguay: Makthlawaiya: BMNH 1927.11.23.55–64 (1*/6). *T. rogoaguae*: Bolivia: Lake Rogoagua: Holotype: CAS 43531 (1); Paratypes: CAS 42532 (39).

## GENUS *PTEROLEBIAS* GARMAN

*Pterolebias* Garman, 1895, p. 141 (type species *Pterolebias longipinnis* Garman, by original designation).

ETYMOLOGY: *Pterolebias* from the Greek *pteros*, meaning wings and *Lebias*, a nominal cyprinodontiform genus, referring to the elongate pelvic fin rays in males.

TYPES: Brazil: Santarem: *Pterolebias longipinnis* Garman Type. USNM 120429 (1).

COMPOSITION: Five species: *longipinnis* Garman; *zonatus* Myers; *peruensis* Myers; *bockermanni* Travassos; and, *hoignei* Thomerson.

DIAGNOSIS: Distinguished from all other aplocheiloids by lacking the interarcual cartilage.

DEFINITION: Anal: ii, 17–ii, 18; Dorsal: ii, 8–ii, 9; Pelvic: 7–8; Pectoral: 15–16; Caudal: 5, 14, 5; Vertebrae: 15+15–15+18. Gill rakers on anterior arm of the first arch: 9; Branchiostegal rays: 6; Scales lateral series: 35–38.

First pleural rib on parapophysis of second vertebra; parapophysis not reduced; no pleural rib on first hemal spine; hypural plates divided, upper plate never divided in two. Epipleural ribs not bifid.

Anal fin not modified into a gonopodium; anal fin musculature unmodified; first proximal radial present; middle anal radials present.

Spermatozeugmata not formed; fertilization external; development annual; oviparous. Eggs round.

One dorsal ray articulating with each of the first two dorsal radials; dorsal fin on posterior third of body.

Autopterotic fossa normal; lateral ethmoid expanded medially, extending under parasphenoid; parasphenoid slightly expanded anteriorly; weakly formed supraoccipital and epiotic processes; neural spine on first vertebra; first vertebra articulates with skull via basioccipital and exoccipital condyles; supraoccipital excluded from formation of foramen magnum; parietals present; nasals not expanded medially.

Mesethmoid cartilaginous; medial processes of pelvic fin base and ischial process reduced; interarcual cartilage absent; second pharyngobranchial which possesses a bony flange; basihyal broad anteriorly, elongate ossification posteriorly; no tooth patches on second and third hypobranchials; teeth on fourth ceratobranchials; dorsal and ventral hypohyal present; anterior extension of anterior ceratohyal ventral to hypohyals; uncinate process on fourth epibranchial articulates with that of third; first epibranchial narrow at its base. Interhyal cartilaginous; three ossified basibranchials. Vomer with posterior extension dorsal to parasphenoid.

Lacrimal narrow and twisted with obsolescent sensory canal; dermosphenotic and preopercular with obsolescent sensory canal; pectoral girdle lowset; first postcleithrum absent; posttemporal with ossified lower limb; posttemporal not fused to supracleithrum.

Vomer ossified, dentigerous; medial arm of maxilla twisted with no pronounced dorsal process; ventral arms with pronounced anterior extension abutting rostral cartilage; outer arm narrow.

Premaxillary ascending processes flat and broad, not tapered posteriorly not overlapping in the midline; rostral cartilage enlarged and rectangular; outer arm of premaxilla with alveolar process, not indented posteriorly. Ligament extending from ventral arms of maxillaries to middle of rostral cartilage; ethmomaxillary ligament present; meniscus present between premaxilla and maxilla.

Dentary not expanded medially, not robust; coronoid process on dentary not overlapping with that of articular; retroarticular not elongate. Autopalatine with straight head, ventral process not elongate, not reaching quadrate; metapterygoid present.

Orbital rim attached; anterior naris tubular; supraorbital sensory pores reduced to a series of neuromasts preopercular, mandibular and lacrimal pores absent, replaced by a series of weakly formed neuromasts. Branchiostegal rays covered.

Males larger than females, often with fin extensions; pelvic fins elongate, extending beyond first four or five anal rays in some species (*longipinnis*). Throat bars not present.

No fatty predorsal ridge; caudal scaled for at least one-third its length; swimbladder extending posteriorly to first one or two hemal spines.

DISTRIBUTION: Lowlands of Peru, Venezuela and Brazil.

REMARKS: The composition of *Pterolebias* was changed by Taphorn and Thomerson (1978) who removed the nominal species *P. maculipinnis* Radda from the genus and placed it in *Rachovia*. The findings of this study agree with such a change.

MATERIAL EXAMINED: *P. longipinnis*: the holotype as listed above; Brazil (Aquarium material): SU 4782-3 (1*/3); Para: AMNH 22466 (2+/2); *P. peruensis*: Peru: E. Loreto Prov: Paratypes: SU 47659 (3); *P. hoignei*: Venezuela: Cojedes: Paratopotypes: CAS 27555 (4); *P. zonatus*: Venezuela: Guarico: AMNH 22467 (1+/1).

## GENUS *RACHOVIA* MYERS

*Rachovia* Myers, 1927, p. 116, 119 (type species *Rivulus brevis* Regan, by original designation).

ETYMOLOGY: *Rachovia* named in honor of Arthur Rachow, an aquarist.

TYPES: Colombia: *Rivulus brevis* Regan, Type BMNH 1908.5.14.8 (1).

COMPOSITION: Four species: *brevis* (Regan); *maculipinnis* (Weibezahn); *hummelincki* de Beaufort; and *pyropunctata* Taphorn and Thomerson.

DIAGNOSIS: Distinguished from all other Neotropical aplocheiloids with a vertical bar through the eye, and a tendency to develop a fatty dorsal ridge by having a low number of scales in a lateral series, generally 32 or less.

DEFINITION: Anal: iii, 11–iii, 12; Dorsal: i, 9–i, 11; Pelvic: 7; Pectoral: 15–16; Caudal: 8, 15, 8; Vertebrae: 12+15–13+17. Gill rakers on anterior arm of the first arch: 9, 10; Branchiostegal rays: 6; Scales lateral series: 27–33.

First pleural rib on parapophysis of second vertebra; parapophysis not reduced; no pleural rib on first hemal spine; hypural plates divided or fused into a fan, upper plate never divided in two. Epipleural ribs not bifid.

Anal fin not modified into a gonopodium; anal fin musculature unmodified; first proximal radial present; middle anal radials present; anal rays of female thickened.

Spermatozeugmata not formed; fertilization external; development annual; oviparous. Eggs round.

One dorsal ray articulating with each of the first two dorsal radials; dorsal fin origin opposite that of anal.

Autopterotic fossa normal; lateral ethmoid expanded medially, extending under parasphenoid; parasphenoid slightly expanded anteriorly; weakly formed supraoccipital and epiotic processes; neural spine on first vertebra; first vertebra articulates with skull via basioccipital and exoccipital condyles; supraoccipital excluded from formation of foramen magnum; parietals present; nasals not expanded medially.

Mesethmoid cartilaginous; medial processes of pelvic fin base and ischial process reduced; interarcual cartilage large, attaches laterally to second pharyngobranchial which possesses a bony flange; basihyal broad anteriorly, elongate ossification posteriorly; no tooth patches on second and third hypobranchials; teeth on fourth ceratobranchials; dorsal and ventral hypohyal present; anterior extension of anterior ceratohyal ventral to hypohyals; uncinate process on fourth epibranchial articulates with that of third; first epibranchial narrow at its base. Interhyal cartilaginous; three ossified basibranchials. Vomer with posterior extension dorsal to parasphenoid.

Lacrimal narrow and twisted with obsolescent sensory canal; dermosphenotic and preopercular with obsolescent sensory canal; pectoral girdle lowset; first postcleithrum absent; posttemporal with ossified lower limb; posttemporal not fused to supracleithrum.

Vomer ossified, dentigerous; medial arm of maxilla twisted with no pronounced dorsal process; ventral arms with pronounced anterior extension abutting rostral cartilage; outer arm narrow.

Premaxillary ascending processes flat and broad, not tapered posteriorly not overlapping in the midline; rostral cartilage enlarged and rectangular; outer arm of premaxilla with alveolar process, not indented posteriorly. Ligament extending from ventral arms of maxillaries to middle of rostral cartilage; ethmomaxillary ligament present; meniscus present between premaxilla and maxilla.

Dentary not expanded medially, not robust; coronoid process on dentary not overlapping with that of articular; retroarticular not elongate. Autopalatine with straight head, ventral process not elongate, not reaching quadrate; metapterygoid present.

Orbital rim attached; anterior naris tubular; supraorbital sensory pores reduced to a series of neuromasts in weakly formed lyre-shaped pattern; preopercular, mandibular and lacrimal pores absent, replaced by a series of weakly formed neuromasts. Branchiostegal rays covered.

Males larger than females, often with fin extensions; males often with light ventral margin of caudal fin; females typically drab; vertical bar through eye; males often with dark blotch on the dorsal.

Fatty predorsal ridge in older males; caudal scaled for more than one third; swimbladder extending posteriorly to first one or two hemal spines.

DISTRIBUTION: Coastal llanos of Venezuela and Colombia.

REMARKS: The composition of the genus *Rachovia* was enlarged by Taphorn and Thomerson (1978) who removed the species *maculipinnis* from *Pterolebias* and placed it in *Rachovia*. This study supports that decision. The genus was most recently revised by Taphorn and Thomerson (1978).

MATERIAL EXAMINED: *R. brevis*: Colombia: the type as listed above; SU 49519 (1*/2); AMNH 22476 (1+); *R. maculipinnis*: Colombia: Meta: CAS 36650 (1*/10).

### GENUS *AUSTROFUNDULUS* MYERS

*Austrofundulus* Myers, 1932, p. 159 (type species *Austrofundulus transilis* Myers, by original designation).

ETYMOLOGY: *Austrofundulus* from *austro*, meaning southern and *Fundulus*, a North American cyprinodontiform genus, in reference to the genus as the *Fundulus* of the Southern Hemisphere.

TYPES: Venezuela: State of Guarico, Orinoco Drainage. *Austrofundulus transilis* Myers, Holotype USNM 92191 (1).

COMPOSITION: Two species: *transilis* Myers, and *limnaeus* Schultz.

DIAGNOSIS: Distinguished from all other aplocheiloids by a darkly pigmented anal papilla.

DEFINITION: Anal: iii, 12–iii, 14; Dorsal: iii, 9–iv, 10; Pelvic: 7; Pectoral: 15–16; Caudal: 8, 16, 8; Vertebrae: 13+17–13+18. Gill rakers on anterior arm of the first arch: 13–15; Branchiostegal rays: 6; Scales lateral series: 28–38.

First pleural rib on parapophysis of second vertebra; parapophysis not reduced; no pleural rib on first hemal spine; hypural plates divided or fused into a fan, upper plate never divided in two. Epipleural ribs not bifid.

Anal fin not modified into a gonopodium; anal fin musculature unmodified; first proximal radial absent; middle anal radials present; anal rays of females thickened.

Spermatozeugmata not formed; fertilization external; development annual; oviparous. Eggs round.

One dorsal ray articulating with each of the first two dorsal radials; dorsal fin origin opposite anal fin origin.

Autopterotic fossa normal; lateral ethmoid expanded medially, extending under parasphenoid; parasphenoid slightly expanded anteriorly; weakly formed supraoccipital and epiotic processes; enlarged neural spine on first vertebra; first vertebra articulates with skull via basioccipital and exoccipital condyles; supraoccipital excluded from formation of foramen magnum; parietals present; nasals not expanded medially.

Mesethmoid cartilaginous; medial processes of pelvic fin base and ischial process reduced; interarcual cartilage large, attaches laterally to second pharyngobranchial which possesses a bony flange; basihyal broad anteriorly, elongate ossification posteriorly; no tooth patches on second and third hypobranchials; teeth on fourth ceratobranchials reduced; dorsal and ventral hypohyal present; anterior extension of anterior ceratohyal ventral to hypohyals; uncinate process on fourth epibranchial articulates with that of third; first epibranchial narrow at its base. Interhyal cartilaginous; three ossified basibranchials. Vomer with posterior extension dorsal to parasphenoid.

Lacrimal narrow and twisted with obsolescent sensory canal; dermosphenotic and preopercular with obsolescent sensory canal; pectoral girdle lowset; first postcleithrum absent; posttemporal with ossified lower limb; posttemporal not fused to supracleithrum.

Vomer ossified, dentigerous; medial arm of maxilla twisted with no pronounced dorsal process; ventral arms with pronounced anterior extension abutting rostral cartilage; outer arm narrow.

Premaxillary ascending processes flat and broad, not tapered posteriorly not overlapping in the midline; rostral cartilage enlarged and rectangular; outer arm of premaxilla with alveolar process, not indented posteriorly. Ligament extending from ventral arms of maxillaries to middle of rostral cartilage; ethmomaxillary ligament present; meniscus present between premaxilla and maxilla.

Dentary not expanded medially, not robust; coronoid process on dentary not overlapping with that of articular; retroarticular not elongate. Autopalatine with straight head, ventral process not elongate, not reaching quadrate; metapterygoid present.

Orbital rim attached; anterior naris tubular; supraorbital sensory pores reduced to a series of neuromasts in weakly formed lyre-shaped pattern; preopercular, mandibular and lacrimal pores absent, replaced by a series of weakly formed neuromasts. Branchiostegal rays covered.

Males larger than females, often with fin extensions; females typically drab; anal papilla heavily pigmented; vertical bar through eye.

Fatty predorsal ridge in older males; caudal scaled for more than one-third its length; swimbladder extending posteriorly to first one or two hemal spines.

DISTRIBUTION: Coastal llanos of Colombia and Venezuela with greatest concentration between the Rio Orinoco and Rio Magdalena.

REMARKS: The genus has been most recently revised by Taphorn and Thomerson (1978).

MATERIAL EXAMINED: *A. transilis*: Venezuela: the holotype as listed above; Falcon: SU 33822 (1*/6); AMNH 22000 (5+/5); Cojedes: FMNH 85725 (3*/17). *A. limnaeus*: Venezuela: Zulia: CAS 39378 (2*/40).

## GENUS *NEOFUNDULUS* MYERS

*Neofundulus* Myers, 1924b, p. 9 (type species *Fundulus paraguayensis* Eigenmann and Kennedy, by original designation).

ETYMOLOGY: *Neofundulus* from the Greek *neos,* meaning new and *Fundulus,* a North American cyprinodontiform genus, meaning a new form of that genus.

TYPES: Paraguay: Arroyo Trematina. *Neofundulus paraguayensis* Eigenmann and Kennedy. Holotype CAS 42533 (1).

COMPOSITION: Solely the type species.

DIAGNOSIS: Distinguished from other Neotropical aplocheiloids with a vertical bar through the eye by a derived pigmentation pattern consisting of rows of dark red reticulations on the sides and dark maroon margins of the caudal and anal fins.

DEFINITION: Anal: iii, 12; Dorsal: i, 12; Pelvic: 7; Pectoral: 16–17; Caudal: 8, 13, 8; Gill rakers on anterior arm of the first arch: 8; Branchiostegal rays: 6; Scales lateral series: 34–38.

First pleural rib on parapophysis of second vertebra; hypural plates divided, upper plate never divided in two.

Anal fin not modified into a gonopodium.

Spermatozeugmata not formed; fertilization external; development annual; oviparous. Eggs round.

Dorsal fin origin opposite that of anal.

Orbital rim attached; anterior naris tubular; supraorbital sensory pores reduced to a series of neuromasts; preopercular, mandibular and lacrimal pores absent, replaced by a series of weakly formed neuromasts. Branchiostegal rays covered.

Males larger than females, often with fin extensions; pigmentation pattern consisting of row of dark red reticulations along the sides of the body and extending on to caudal and anal fins.

No fatty predorsal ridge; caudal scaled for at least one third its length.

DISTRIBUTION: That of the holotype.

REMARKS: The meristic data for the genus were recorded from the alcohol specimen (the type) and supplemented by the species description. The color pattern described is from de Souza (1979), from which information on osteology and distribution also was obtained.

Arambaru, Arambaru and Ringuelit (in de Souza, 1979) suggested the species previously referred to the genus, *paraguayensis* and *ornatipinnis,* be synonymized. This is not recommended considering their scant sample sizes and the poor condition of museum specimens. The holotype of *paraguayensis* is a female and that of *ornatipinnis* a male, so from the type material alone, it is impossible to determine whether the differences are due to sexual dimorphism. However, data and photographs of *paraguayensis* in de Souza (1979) indicate that in both males and females the meristic counts are lower than in the *ornatipinnis* holotype.

MATERIAL EXAMINED: The holotype as listed above.

## GENUS "*NEOFUNDULUS*"

ETYMOLOGY: "*Neofundulus*" is used to reference the more derived species of the genus *Neofundulus*.

COMPOSITION: A single species, *ornatipinnis* Myers.

TYPES: Paraguay: *Neofundulus ornatipinnis* Myers, Holotype, USNM 94401 (1).

DEFINITION: Anal: iii, 12; Dorsal: ii, 13; Pelvic: 7; Pectoral: 16–17; Caudal: 8, 13, 8; Vertebrae: 13+15. Gill rakers on anterior arm of the first arch: 8, 9; Branchiostegal rays: 6; Scales lateral series: 37.

Anal fin not modified into a gonopodium.

Spermatozeugmata not formed; fertilization external; development annual; oviparous. Eggs round.

Dorsal fin origin opposite that of anal.

Orbital rim attached; anterior naris tubular; supraorbital sensory pores reduced to a series of neuromasts; preopercular, mandibular and lacrimal pores absent, replaced by a series of weakly formed neuromasts. Branchiostegal rays covered.

No fatty predorsal ridge; caudal scaled for at least one-third its length.

DISTRIBUTION: That of the holotype.

REMARKS: The species in "*Neofundulus*" is more closely related to the more derived genera of *Austrofundulus* and *Cynolebias* than it is to *Neofundulus paraguayensis*. Since the condition of the specimen is poor, it is not considered appropriate to create a new genus based on the specimen to which the temporary name of "*Neofundulus*" is applied.

## GENUS *CYNOLEBIAS* STEINDACHNER

*Cynolebias* Steindachner, 1876, p. 172 (type species *Cynolebias porosus* Steindachner, by original designation).

*Cynopoecilus* Regan, 1912, p. 642 (type species *Cynolebias melanotaenia* Regan, by original designation).

*Leptolebias* Myers, 1952, p. 140 (type species *Cynolebias marmoratus* Ladiges, by original designation [proposed as a subgenus]).

*Simpsonichthys* de Carvalho, 1959, p. 2 (type species *Simpsonichthys boitonei* de Carvalho, by original designation).

*Campellolebias* Vaz-Ferreira and Sierra, 1974, p. 1 (type species *Campellolebias brucei* Vaz-Ferreira and Sierra, by original designation).

*Terranotus* Taphorn and Thomerson, 1978, p. 384 (type species *Austrofundulus dolichopterus* Weitzman and Wourms, by original designation).

ETYMOLOGY: *Cynolebias* from the Greek *cyno,* meaning dog and *Lebias*, a synonym of another cyprinodontiform genus, referring to the robust outer teeth in the lower jaw referred to as canines and suggesting a dog.

COMPOSITION: Approximately 35 species, referable to the above synonyms (Lazara, 1979).

DIAGNOSIS: Distinguished from all other aplocheiloids by having a preopercular canal which is completely closed.

DEFINITION: Anal: ii, 14; Dorsal: iii, 11–ii, 16; Pelvic: 7; Pectoral: 13–14; Caudal: 7, 19, 7; Vertebrae: 13+16–15+22. Gill rakers on anterior arm of the first arch: 9–17; Branchiostegal rays: 6; Scales lateral series: 23–60.

First pleural rib on parapophysis of second vertebra; parapophysis not reduced; no pleural rib on first hemal spine; hypural plates fused to form an hypural fan. Epipleural ribs not bifid.

Anal fin modified into a gonopodium in a sole species (*brucei*); anal fin musculature unmodified; first proximal radial absent; middle anal radials present; anal rays of females thickened.

Spermatozeugmata not formed; fertilization external in all but two species (*brucei* and *melanotaenia*); development annual; oviparous. Eggs round.

One dorsal ray articulating with each of the first two dorsal radials; dorsal fin on posterior third of body.

Autopterotic fossa normal; lateral ethmoid expanded medially, extending under parasphenoid; parasphenoid slightly expanded anteriorly; weakly formed supraoccipital and epiotic processes; enlarged neural spine on first vertebra; first vertebra articulates with skull via basioccipital and exoccipital condyles; supraoccipital excluded from formation of foramen magnum; parietals present; nasals not expanded medially.

Mesethmoid cartilaginous; medial processes of pelvic fin base and ischial process reduced; interarcual cartilage large, attaches laterally to second pharyngobranchial which possesses a bony flange; basihyal broad anteriorly, elongate ossification posteriorly; no tooth patches on second and third hypobranchials; teeth on fourth ceratobranchials reduced or absent; dorsal and ventral hypohyal present; anterior extension of anterior ceratohyal ventral to hypohyals; uncinate process on fourth epibranchial articulates with that of third; first epibranchial narrow at its base. Interhyal cartilaginous; three ossified basibranchials. Vomer with posterior extension dorsal to parasphenoid.

Lacrimal narrow and twisted with obsolescent sensory canal; dermosphenotic and preopercular with obsolescent sensory canal; pectoral girdle lowset; first postcleithrum absent; posttemporal with ossified lower limb; posttemporal not fused to supracleithrum.

Vomer ossified, dentigerous; medial arm of maxilla twisted with no pronounced dorsal process; ventral arms with pronounced anterior extension abutting rostral cartilage; outer arm narrow.

Premaxillary ascending processes flat and broad, not tapered posteriorly not overlapping in the midline; rostral cartilage enlarged and rectangular; outer arm of premaxilla with alveolar process, not indented posteriorly. Ligament extending from ventral arms of maxillaries to middle of rostral cartilage; ethmomaxillary ligament present; meniscus present between premaxilla and maxilla.

Dentary not expanded medially, not robust; coronoid process on dentary not overlapping with that of articular; retroarticular not elongate. Autopalatine with straight head, ventral process not elongate, not reaching quadrate; metapterygoid present.

Orbital rim attached; anterior naris tubular; supraorbital sensory pores reduced to a series of neuromasts in distinctive lyre-shaped pattern; preopercular, mandibular, and lacrimal pores absent, replaced by a series of weakly formed neuromasts. Brànchiostegal rays covered.

Males larger than females, rarely with fin extensions; no species with a spot at the anterior base of the dorsal fin; middle rays of caudal never elongate in juveniles and adults; vertical bar through eye.

Fatty predorsal ridge in at least one species (*dolichopterus*); caudal fin not scaled; swimbladder extending posteriorly to first one or two hemal spines.

DISTRIBUTION: Cojedes, Venezuela; lowlands of Argentina, Brazil and Paraguay.

REMARKS: Species of *Cynolebias* have been isolated in genera or subgenera on the basis of their apomorphous characters. Taphorn and Thomerson (1978) stated that *Terranotus dolichopterus* perhaps was more closely related to *Cynolebias* than to either *Austrofundulus* or *Rachovia*.

A subgroup of species may be defined by having a higher number of dorsal and anal fin rays in males. However, subgroups are not named since a revision of the genus is judged to be a necessary prerequisite to such taxonomic decisions. Since a name placed in synonymy herein may be suitable for some subgroup of *Cynolebias*, new names are not produced in the interest of minimizing synonyms.

Ahl (1934) reviewed *Cynolebias*; the definition, distribution and composition of the genus again were reviewed by Vaz-Ferreira and Sierra (1973).

MATERIAL EXAMINED: *C. belottii*: Argentina: Buenos Aires: USNM 176105 (17); *C. elongatus*: Argentina: Villa Elisa: SU 64048 (2*/9); *C. melanotaenia*: Brazil: Porto Alegre: SU 64060 (2*/8), Paranagua: Types: BMNH 1909.9.5.15–22 (8); *C. boitonei*: Aquarium material: AMNH 38431 (3); *C. whitei*: Aquarium material: AMNH 36769 (4*/8); *C. brucei*: Brazil: Santa Catarina: ZVC,P. 2123 (1), ZVC, P. 2121 (1); *C. ladigesi*: Brazil: Paratypes: SU 50177 (2); *C. dolichopterus*: Venezuela: Cojedes: Holotype: USNM 200784 (1); Paratypes: AMNH 22718 (3); FMNH: 85726 (1*/5).

## SUBORDER CYPRINODONTOIDEI

DIAGNOSIS: Distinguished from the aplocheiloid cyprinodontiforms by 12 uniquely derived characters: two basibranchials in the ventral gill arch skeleton; loss of the dorsal hypohyal; reduction of the interarcual cartilage to approximately half its length with the placement of the first epibranchial closer to the second pharyngobranchial; an autopalatine with anterior arm offset to the main axis and a weakly to strongly formed posterior flange; a ventral extension of the autopalatine forming an anterior covering of the quadrate; metapterygoid absent; premaxilla with a posterior indentation of the alveolar arm to form an S-shaped distal arm; a dentary expanded medially to form a robust lower jaw; loss of the first dorsal ray so that the first dorsal fin ray articulates with the first two proximal radials; loss of the ethmomaxillary ligament; loss of a ligament from the interior arms of the maxilla to the middle of the rostral cartilage; and, the absence of a meniscus between the premaxilla and maxilla.

## SECTION 1

### FAMILY PROFUNDULIDAE HOEDEMAN AND BRONNER

Type Genus *Profundulus* Hubbs, 1924.

DIAGNOSIS: Distinguished from all other cyprinodontoids by a large autopterotic fossa, and a high number of gill rakers on the anterior arm of the first arch (14–23).

COMPOSITION: One genus, *Profundulus*, with five species: *candalarius* Hubbs, *guatemalensis* (Günther), *hildebrandi* Miller, *labialis* (Günther), and *punctatus* (Günther).

DISTRIBUTION: Both Atlantic and Pacific slopes of Middle America. Atlantic slope: Guatemala: Isthmus of Tehuantepec to the Rio Motagua; Pacific slope: Rio Papagaya, Guerrero, Mexico to Rio Lempa drainage, Honduras (fig. 74).

### GENUS *PROFUNDULUS* HUBBS

*Profundulus* Hubbs, 1924, p. 12 (type species *Fundulus punctatus* Günther, by original designation).

*Tlaloc* Alvarez and Carranza, 1951, p. 40 (type species *Fundulus labialis* Günther by monotypy).

ETYMOLOGY: *Profundulus* in reference to its presumed primitive relationship to the genus *Fundulus*.

TYPES: Guatemala: Chiapas: *Fundulus punctatus* Günther; Types, BMNH 1864. 1.26. 187A–C (3).

COMPOSITION: As for the family.

DIAGNOSIS: As for the family.

DEFINITION: Anal: (0–iii) 11–18; Dorsal: (i–iii) 10–16; Pelvic: 5–7; Pectoral: 15–22; Caudal: 17–25; Vertebrae: 15+16–16+23; Gill rakers on anterior arm of the first arch: 14–23. Branchiostegal rays: 6; Scales lateral series: 31–39.

First pleural rib on parapophysis of second vertebra; parapophysis not reduced; no pleural ribs on hemal spines; hypural plates slightly divided in midline. Epipleural ribs not bifid.

Anal fin not modified into a gonopodium; anal fin musculature unmodified; first proximal radial present; middle anal radials present.

Spermatozeugmata not formed; fertilization external; development nonannual; oviparous. Eggs round.

One dorsal ray articulating with the first two dorsal radials; dorsal fin origin opposite origin of anal.

Autopterotic fossa large; lateral ethmoid not expanded medially, not reaching parasphenoid; parasphenoid not expanded anteriorly; no supraoccipital and exoccipital processes; neural arches of first vertebra open, not forming a spine; first vertebra articulates with skull via basioccipital and exoccipital condyles; supraoccipital excluded from formation of foramen magnum; parietals present; nasals not expanded medially. Lateral ethmoid with reduced anterior facet.

Mesethmoid ossified; medial processes of pelvic fin base and ischial process not reduced; interarcual cartilage reduced, attaches laterally to second pharyngobranchial with a bony flange; basihyal long and narrow; no tooth patches on second and third hypobranchials; teeth on fourth ceratobranchials; dorsal hypohyal absent; anterior extension of anterior ceratohyal ventral to ventral hypohyal; uncinate process on fourth epibranchial articulates with that of third; first epibranchial wide at its base; interhyal ossified; two ossified basibranchials. Vomer with posterior extension ventral to parasphenoid.

Lacrimal flat and broad, carrying a distinct sensory canal; dermosphenotic and preopercular with distinct sensory canal; pectoral girdle lowset; first postcleithrum present; posttemporal with ossified lower limb; posttemporal not fused to supracleithrum.

Vomer ossified, edentulous; medial arm of maxilla twisted with no pronounced dorsal process; ventral arms gently curved toward and abutting rostral cartilage; outer arm narrow.

Premaxillary ascending processes flat and broad, not tapered posteriorly and not overlapping in the midline; rostral cartilage large and rectangular; outer arm of premaxilla with alveolar process, indented posteriorly to form S-shaped arm. No ligament from the ventral arms of maxillaries to middle of rostral cartilage; no ethmomaxillary ligament; no meniscus between premaxilla and maxilla. Unicuspid bi- or triserial outer teeth.

Dentary expanded medially, robust; coronoid process on dentary not overlapping with that of articular; retroarticular not elongate. Autopalatine with head angled anteriorly; ventral process elongate reaching quadrate; metapterygoid absent.

Orbital rim free; anterior naris slightly tubular; supraorbital sensory pores 1–2a, 2b–4a, 4b–7; seven preopercular pores; four mandibular pores; 3 lacrimal pores.

Females larger than males; males never with fin extensions; middle rays of caudal never elongate; no throat bars present.

No fatty predorsal ridge; swimbladder does not extend posteriorly beyond hemal spines.

DISTRIBUTION: As for the family.

REMARKS: The genus is the most plesiomorphic cyprinodontoid, a conclusion that supports Hubbs (1924).

*Profundulus* has been most recently reviewed by Miller (1955a) from which ranges of meristic data have been supplemented.

MATERIAL EXAMINED: *P. punctatus*: Guatemala: the types as listed above; Sachitepequez: AMNH 32306 (3*/30); AMNH 24432 (1+/1). *P. labialis*: Guatemala: AMNH 24567 (2+/2); Baja Verapaz: AMNH 22896 (240). *P. guatemalensis*: Guatemala: Rio La Conquista: AMNH 31721 (4).

## SECTION 2

DIAGNOSIS: Distinguished from *Profundulus* and the aplocheiloids by the following derived characters: premaxillary ascending processes narrow or absent in adults; rostral cartilage greatly reduced or absent; inner arms of the maxillaries not abutting rostral cartilage, and remaining attached to it by connective tissue; and, the lateral ethmoid lacking or with a greatly reduced facet for articulation of the autopalatine.

## DIVISION 1

## FAMILY FUNDULIDAE JORDAN AND GILBERT

Type Genus *Fundulus* Lacépède, 1803.

DIAGNOSIS: Distinguished from all other members of the suborder Cyprinodontoidei by the anteriorly directed ventral arms of the maxillaries often with pronounced hooks; snout pointed and drawn anteriorly; and autopalatine projecting anterior to the lateral ethmoid.

COMPOSITION: Five genera comprising approximately 40 species (Lazara, 1979): *Fundulus* Lacépède; *Plancterus* Garman; *Lucania* Girard; *Adinia* Girard; and *Leptolucania* Myers.

DISTRIBUTION: Lowlands of North and Middle America, southward to Yucatan; Bermuda and Cuba (fig. 76).

## GENUS *PLANCTERUS* GARMAN

*Plancterus* Garman, 1895, p. 96 (type species *Hydrargyra kansae* Garman, by original designation).

*Fontinus* Jordan and Evermann, 1896, p. 645 (type species *Fundulus zebrinus* Jordan and Gilbert, by monotypy).

ETYMOLOGY: *Plancterus* from the Greek *planktos*, meaning wandering.

COMPOSITION: Two species: *zebrinus* (Jordan and Gilbert) and *kansae* (Garman).

DIAGNOSIS: Distinguished from all other members of the family Fundulidae by the derived character of a greatly convoluted intestine.

DEFINITION: Anal: i, 11; Dorsal: ii, 11; Pelvic: 6; Pectoral: 17–18; Caudal: 8, 16, 8; Vertebrae: 14+18; Gill rakers on the anterior arm of the first arch: 8. Branchiostegal rays: 6; Scales lateral series: 60–63.

First pleural rib on parapophysis of second vertebra; parapophysis not reduced; no pleural ribs on hemal spines; hypural plates fused into hypural fan. Epipleural ribs not bifid.

Anal fin not modified into a gonopodium; anal fin musculature unmodified; first proximal radial present; middle anal radials present.

Spermatozeugmata not formed; fertilization external; development nonannual; oviparous. Eggs round.

One dorsal ray articulating with the first two dorsal radials; dorsal fin origin opposite origin of anal.

Autopterotic fossa moderate; lateral ethmoid not expanded medially, not reaching parasphenoid; parasphenoid not expanded anteriorly; normal supraoccipital and exoccipital processes; neural arches of first vertebra open, not forming a spine; first vertebra articulates with skull via basioccipital and exoccipital condyles; supraoccipital excluded from formation of foramen magnum; parietals present; nasals not expanded medially. Lateral ethmoid with reduced anterior facet.

Mesethmoid ossified; medial processes of pelvic fin base and ischial process not reduced; interarcual cartilage reduced, attaches laterally to second pharyngobranchial with a bony flange; basihyal long and narrow; no tooth patches on second and third hypobranchials; teeth on fourth ceratobranchials; dorsal hypohyal absent; anterior extension of anterior ceratohyal ventral to ventral hypohyal; uncinate process on fourth epibranchial articulates with that of third; first epibranchial wide at its base; interhyal ossified; two ossified basibranchials. Vomer with posterior extension ventral to parasphenoid.

Lacrimal flat and broad, carrying a distinct sensory canal; dermosphenotic and preopercular with distinct sensory canal; pectoral girdle lowset; first postcleithrum present; posttemporal with ossified lower limb; posttemporal not fused to supracleithrum.

Vomer ossified, edentulous; medial arm of maxilla twisted with no pronounced dorsal process; ventral arms projecting anteriorly with pronounced hooks, not abutting rostral cartilage; outer arm narrow.

Premaxillary ascending processes narrow and elongate, not tapered posteriorly and not overlapping in the midline; rostral cartilage reduced; outer arm of premaxilla with alveolar process, indented posteriorly to form S-shaped arm. No ligament from the ventral arms of maxillaries to middle of rostral cartilage; no ethmomaxillary ligament; no meniscus between premaxilla and maxilla. Unicuspid bi- or tri-serial outer teeth.

Dentary expanded medially, robust; coronoid process on dentary not overlapping with that of articular; retroarticular not elongate. Autopalatine with head angled anteriorly; ventral process elongate reaching quadrate; metapterygoid absent.

Orbital rim free; anterior naris not tubular; supraorbital sensory pores 1–2a, 2b–4a, 4b–7; seven preopercular pores; four mandibular pores; three lacrimal pores.

Females larger than males; males never with fin extensions; middle rays of caudal not elongate; pigmentation pattern consisting of several silvery crossbars on the sides.

No fatty predorsal ridge; swimbladder does not extend posteriorly beyond hemal spines.

DISTRIBUTION: Texas and Mexico: Brazos, Colorado and Pecos drainages; Llano Estacado, Texas; Great Plains of South Dakota (possible introduction) to Red and Arkansas rivers, Texas and New Mexico, respectively.

REMARKS: The species of the formerly ranked subgenus *Plancterus* are treated as a genus in this study since they have been excluded from the monophyletic group including the other species of *Fundulus* and the other funduline genera. Distribution data are from Miller (1955b).

MATERIAL EXAMINED: *P. kansae*: Oklahoma: Major Co.: AMNH 28600 (2+/12); Kansas: AMNH 27278 (384); *P. zebrinus*: AMNH 7781 (2+/2).

### GENUS *FUNDULUS* LACÉPÈDE

*Fundulus* Lacépède, 1803, p. 37 (type species *Cobitus heteroclita* Linnaeus, by monotypy).

*Hydrargira* Lacépède, 1803, p. 378 (type species *Hydrargira swampina* Lacépède, by monotypy).

*Hydrargyra* Rafinesque, 1815, p. 88 (emended spelling of *Hydrargira* Lacépède).

*Zygonectes* Agassiz, 1853, p. 135 (type species *Poecilia olivacea* Storer, by original designation).

*Micristius* Gill, 1865, p. 24 (type species *Fundulus cingulatus* Valenciennes, by original designation).

*Xenisma* Jordan, 1876, p. 142 (type species *Fundulus stellifer* Jordan, by original designation).

*Borborys* (Broussonet) Goode and Bean, 1885, p. 204 (type species *Cobitus heteroclita* Linnaeus, by monotypy).

*Gambusinus* Jordan and Evermann, 1896, p. 649 (type species *Fundulus rathbuni* Jordan and Meek, by original designation).

*Galasaceus* Fowler, 1916, p. 417 (type species *Hydragyra similis* Baird and Girard, by original designation [proposed as a substitute for *Hydrargyra* as commonly used to reference *H. swampina*]).

ETYMOLOGY: *Fundulus* from the Latin *fundus,* meaning bottom referring to the habitat of the type species.

COMPOSITION: Approximately 40 species as listed in Lazara (1979).

DIAGNOSIS: Distinguished from all other cyprinodontiforms by the enlarged cartilaginous articulation point of the second pharyngobranchial.

DEFINITION: Anal: 8–16; Dorsal: i, 11–15; Pelvic: 6; Pectoral: 15–20; Caudal: 6, 15, 6; Vertebrae: 15+16–16+22; Gill rakers on the anterior arm of the first arch: 6–12. Branchiostegal rays: 5–6; Scales lateral series: 34–48.

First pleural rib on parapophysis of second vertebra; parapophysis not reduced; no pleural ribs on hemal spines; hypural plates fused into an hypural fan. Epipleural ribs not bifid.

Anal fin not modified into a gonopodium; anal fin musculature unmodified; first proximal radial present; middle anal radials present.

Spermatozeugmata not formed; fertilization external; development nonannual; oviparous. Eggs round.

One dorsal ray articulating with the first two dorsal radials; dorsal fin origin opposite origin of anal.

Autopterotic fossa moderate; lateral ethmoid not expanded medially, not reaching parasphenoid; parasphenoid not expanded anteriorly; normal supraoccipital and exoccipital processes; neural arches of first vertebra open, not forming a spine; first vertebra articulates with skull via basioccipital and exoccipital condyles; supraoccipital excluded from formation of foramen magnum; parietals present; nasals not expanded medially. Lateral ethmoid with reduced anterior facet.

Mesethmoid ossified; medial processes of pelvic fin base and ischial process not reduced; interarcual cartilage reduced, attaches laterally to expanded articulation point of second pharyngobranchial with a bony flange; basihyal long and narrow; no tooth patches on second and third hypobranchials; teeth on fourth ceratobranchials; dorsal hypohyal absent; anterior extension of anterior ceratohyal ventral to ventral hypohyal; uncinate process on fourth epibranchial articulates with that of third; first epibranchial wide at its base; interhyal ossified; two ossified basibranchials. Vomer with posterior extension ventral to parasphenoid.

Lacrimal flat and broad, carrying a distinct sensory canal; dermosphenotic and preopercular with distinct sensory canal; pectoral girdle lowset; first postcleithrum present; posttemporal with unossified lower limb; posttemporal not fused to supracleithrum.

Vomer ossified, edentulous; medial arm of maxilla twisted with no pronounced dorsal process; ventral arms projecting anteriorly often with pronounced hooks, not abutting rostral cartilage; outer arm narrow.

Premaxillary ascending processes narrow and elongate, not tapered posteriorly and not overlapping in the midline; rostral cartilage reduced; outer arm of premaxilla with alveolar process, indented posteriorly to form S-shaped arm. No ligament from the ventral arms of maxillaries to middle of rostral cartilage; no ethmomaxillary ligament; no meniscus between premaxilla and maxilla. Unicuspid bi- or tri-serial outer teeth.

Dentary expanded medially, robust; coronoid process on dentary not overlapping with that of articular; retroarticular not elongate. Autopalatine with head angled anteriorly; ventral process elongate reaching quadrate; metapterygoid absent.

Orbital rim free; anterior naris not tubular; supraorbital sensory pores 1–2a, 2b–4a, 4b–7; seven preopercular pores; four mandibular pores; 3 lacrimal pores.

Females larger than males; males never with fin extensions; middle rays of caudal never elongate.

No fatty predorsal ridge; swimbladder does not extend posteriorly beyond hemal spines.

DISTRIBUTION: As for the family.

REMARKS: The genus *Fundulus* as constituted herein is a monophyletic group. There has been no decision made to recognize individual components of the genus as separate genera or subgenera since this is a problem for a future revisor.

The genus has been most recently reviewed by Miller (1955b) and Brown (1957). A rediagnosis and comparison with the genera *Empetrichthys* and *Crenichthys* as well as *Profundulus* was given by Uyeno and Miller (1962). Farris (1968) presented a phylogenetic analysis of the species of *Profundulus* and *Fundulus*. Wiley and Hall (1975) and Wiley (1977) have performed phylogenetic analyses of the species of the *F. nottii*-complex and its close relatives. Ranges for meristic data are supplemented by data from Garman (1895) and Miller (1955b).

MATERIAL EXAMINED: *F. heteroclitus*: New York: Sheepshead Bay: AMNH 21916 (2+/2); Columbia Co. AMNH 26464 (3). Aquarium material AMNH 38414 (2*/2). *F. diaphanus*: New York: Grassy Pt. AMNH 10209SW (2*). *F. grandis*: Florida: AMNH 21915SW (1+); Alabama: AMNH 3570 (9). *F. similis*: Florida: AMNH 21919SW (1+). *F. chrysotus*: Florida: AMNH 21911SW (1+); *F. catenatus*: Oklahoma: AMNH 28589SW (2+). *F. confluentus*: Florida: AMNH 21913SW (2+). *F. majalis*: New York: AMNH 28526 (2+); AMNH 28532 (11). *F. olivaceus*: Oklahoma: AMNH 28599 (2+/11). *F. parvipinnis*: California: AMNH 37743 (7). *Zygonectes dispar*: Missouri. Types: USNM 120298 (4).

FOSSILS: Fossil fundulines generally are placed hesitantly in *Fundulus* (Lugaski, 1977; Miller, 1945). The following genus has also been named for such fossils.

## GENUS *PARAFUNDULUS* EASTMAN

*Parafundulus* Eastman, 1917, p. 291 (type species *Parafundulus nevadensis* Eastman, by original designation). (Pleistocene of Nevada)

Farris (1968) identified some specimens of this genus as members of *Profundulus*; however, since he presented no unique characters to define either genus, such an identification is suspect.

## GENUS *LUCANIA* GIRARD

*Lucania* Girard, 1859, p. 118 (type species *Cyprinodon parvus* Baird, by monotypy).

*Chriopeops* Fowler, 1916, p. 425 (type species *Cyprinodon goodei* Jordan, by original designation [proposed as a subgenus]).

ETYMOLOGY: The genus *Lucania*, named by Girard, is of no known significance.

TYPES: New York: Greenport: *Cyprinodon parvus* Baird: USNM 15280 (1).

COMPOSITION: Three species: *parva* (Baird); *goodei* (Jordan); and *interiorus* Hubbs and Miller.

DIAGNOSIS: Distinguished from all other cyprinodontiforms by an independent block of cartilage between the interarcual cartilage and articulation point of the second pharyngobranchial.

DEFINITION: Anal: i, 8–i, 9; Dorsal: i, 11; Pelvic: 6; Pectoral: 12–13 Caudal: 8, 13, 8; Vertebrae: 12+14; Gill rakers on the anterior arm of the first arch: 8–9. Branchiostegal rays: 6; scales lateral series: 27–29.

First pleural rib on parapophysis of second vertebra; parapophysis not reduced; no pleural ribs on hemal spines; hypural plates fused into hypural fan. Epipleural ribs not bifid.

Anal fin not modified into a gonopodium; anal fin musculature unmodified; first proximal radial present; middle anal radials present.

Spermatozeugmata not formed; fertilization external; development nonannual; oviparous. Eggs round.

One dorsal ray articulating with the first two dorsal radials; dorsal fin origin opposite origin of anal.

Autopterotic fossa moderate; lateral ethmoid not expanded medially, not reaching parasphenoid; parasphenoid not expanded anteriorly; normal supraoccipital and exoccipital processes; neural arches of first vertebra open, not forming a spine; first vertebra articulates with skull via basioccipital and exoccipital condyles; supraoccipital excluded from formation of foramen magnum; parietals present; nasals not expanded medially. Lateral ethmoid with reduced anterior facet.

Mesethmoid ossified; medial processes of pelvic fin base and ischial process not reduced; interarcual cartilage reduced, attaches laterally by a block of cartilage to second pharyngobranchial which possesses a bony flange; basihyal long and narrow; no tooth patches on second and third hypobranchials; teeth on fourth ceratobranchials; dorsal hypohyal absent; anterior extension of anterior ceratohyal ventral to ventral hypohyal; uncinate process on fourth epibranchial articulates with that of third; first epibranchial wide at its base; interhyal ossified; two ossified basibranchials. Vomer with posterior extension ventral to parasphenoid.

Lacrimal flat and broad, carrying a distinct sensory canal; dermosphenotic and preopercular with distinct sensory canal; pectoral girdle lowset; first postcleithrum present; posttemporal with ossified lower limb; posttemporal not fused to supracleithrum.

Vomer ossified, edentulous; medial arm of maxilla twisted with no pronounced dorsal process; ventral arms projecting anteriorly, with pronounced hooks, not abutting rostral cartilage; outer arm narrow.

Premaxillary ascending processes narrow and elongate, not tapered posteriorly and not overlapping in the midline; rostral cartilage reduced; outer arm of premaxilla with alveolar process, indented posteriorly to form S-shaped arm. No ligament from the ventral arms of maxillaries to middle of rostral cartilage; no ethmomaxillary ligament; no meniscus between premaxilla and maxilla. Unicuspid uni- bi- or tri-serial outer teeth.

Dentary expanded medially, robust; coronoid process on dentary not overlapping with that of articular; retroarticular not elongate. Autopalatine with head angled anteriorly; ventral process elongate reaching quadrate; metapterygoid absent.

Orbital rim free; anterior naris not tubular: supraorbital canal continuous between pores 1 through 7; seven preopercular pores; four mandibular pores; three lacrimal pores.

Females larger than males; all fins rounded, never extensions; *parva* males with an ocellus at anterior base of dorsal fin; *goodei* with a dark lateral band extending through the eye to base of the caudal fin.

No fatty predorsal ridge; swimbladder does not extend beyond hemal spines.

DISTRIBUTION: Coastal lowlands of northeastern North America; Cuatro Cienegas Basin, Mexico; introduced in California and Texas.

REMARKS: The genus *Lucania* has often been referred to as a presumed close relative of *Cubanichthys* of Cuba, and possibly of *Chriopeoides* of Jamaica (Hubbs and Miller, 1965; Rosen, 1976). However, it has been found that the two island forms are not closely related to the genus *Lucania* nor to any other funduline genus but are rather more derived cyprinodonts related to an assemblage including the Old World and New World cyprinodontines and *Orestias*.

MATERIAL EXAMINED: *L. parva*: New York: the type as listed above; AMNH 35922SW (4*/1071); AMNH 27462SW (5+); *L. goodei*: Florida: Punta Gorda: ANSP 91218 (12); Little Springs: AMNH 22082SW (8+); St. John's R.: Types USNM 23505 (2).

### GENUS *LEPTOLUCANIA* MYERS

*Leptolucania* Myers, 1924b, p. 8 (type species *Heterandria ommata* Jordan, by original designation [proposed as a subgenus]).

ETYMOLOGY: *Leptolucania* from the Greek *lepto,* meaning thin or elongate, and *Lucania,* another funduline genus, referring to the elongate body form.

TYPES: Florida: *Heterandria ommata* Jordan, Type, USNM 25331 (1).

COMPOSITION: Solely the type species.

DIAGNOSIS: Distinguished from all other cyprinodontiform genera by three branchiostegal rays and a unique color pattern consisting of an ocellus on the caudal peduncle and one at midbody. Distinguished from all other fundulid genera in lacking the first postcleithrum.

DEFINITION: Anal: ii, 8; Dorsal: i, 6, Pelvic: 6; Pectoral: 13–14; Caudal: 6, 10, 6; Vertebrae: 12+15; Gill rakers on the anterior arm of the first arch: 6–7. Branchiostegal rays: 6; Scales lateral series: 25–26.

First pleural rib on parapophysis of second vertebra; parapophysis not reduced; no pleural ribs on hemal spines; hypural plates fused into hypural fan. Epipleural ribs not bifid.

Anal fin not modified into a gonopodium; anal fin musculature unmodified; first proximal radial present; middle anal radials present.

Spermatozeugmata not formed; fertilization external; development nonannual; oviparous. Eggs round.

One dorsal ray articulating with the first two dorsal radials; dorsal fin origin opposite origin of anal.

Autopterotic fossa moderate; lateral ethmoid not expanded medially, not reaching parasphenoid; parasphenoid not expanded anteriorly; no supraoccipital and exoccipital processes; neural arches of first vertebra open, not forming a spine; first vertebra articulates with skull via basioccipital and exoccipital condyles; supraoccipital excluded from formation of foramen magnum; parietals present; nasals not expanded medially. Lateral ethmoid with reduced anterior facet.

Mesethmoid ossified; medial processes of pelvic fin base and ischial process not reduced; interarcual cartilage reduced, attaches laterally to second pharyngobranchial with a bony flange; basihyal long and narrow; no tooth patches on second and third hypobranchials; teeth on fourth ceratobranchials; dorsal hypohyal absent; anterior extension of anterior ceratohyal ventral to ventral hypohyal; uncinate process on fourth epibranchial articulates with that of third; first epibranchial wide at its base; interhyal ossified; two ossified basibranchials. Vomer with posterior extension ventral to parasphenoid.

Lacrimal flat and broad, carrying a distinct sensory canal; dermosphenotic and preopercular with distinct sensory canal; pectoral girdle lowset; first postcleithrum absent; posttemporal with ossified lower limb; posttemporal not fused to supracleithrum.

Vomer ossified, edentulous; medial arm of maxilla twisted with no pronounced dorsal process; ventral arms projecting anteriorly with pronounced hooks, not abutting rostral cartilage; outer arm narrow.

Premaxillary ascending processes narrow and elongate, not tapered posteriorly and not overlapping in the midline; rostral cartilage reduced; outer arm of premaxilla with alveolar process, indented posteriorly to form S-shaped arm. No ligament from the ventral arms of maxillaries to middle of rostral cartilage; no ethmomaxillary ligament; no meniscus between premaxilla and maxilla. Unicuspid bi- or triserial outer teeth.

Dentary expanded medially, robust; coronoid process on dentary not overlapping with that of articular; retroarticular not elongate. Autopalatine with head angled anteriorly; ventral process elongate reaching quadrate; metapterygoid absent.

Orbital rim free; anterior naris not tubular; supraorbital sensory pores 6–7; seven preopercular pores; four mandibular pores; three lacrimal pores.

Females larger than males; males never with fin extensions. Pigmentation pattern consisting of a dark blotch at midbody and a midcaudal ocellus.

No fatty predorsal ridge; swimbladder does not extend posteriorly beyond hemal spines.

DISTRIBUTION: Florida and Georgia.

REMARKS: The genus *Leptolucania* has been confused with a diminutive poeciliid *Heterandria formosa,* also of Florida, the genus in which *ommata* was placed when described.

MATERIAL EXAMINED: Florida: the types as listed above; Leon Co.: AMNH 20383 (6+/4*/118).

### GENUS *ADINIA* GIRARD

*Adinia* Girard, 1859, p. 117 (type species *Adinia multifasciata* Girard, by original designation).

ETYMOLOGY: The genus *Adinia,* named by Girard, is of no known significance.

TYPES: Texas: Indianola: *Adinia multifasciata* Girard, Cotypes, ANSP 7291, 7292.

COMPOSITION: Two species: *multifasciata* Girard and *xenica* (Jordan and Gilbert).

DIAGNOSIS: Distinguished from all other cyprinodontiforms by the first pleural rib on the parapophysis of the first vertebra, rather than the second and a distinct quadrangular body form.

DEFINITION: Anal: ii, 8; Dorsal: ii, 7; Pelvic: 6; Pectoral: 17; Caudal: 8, 14, 8; Vertebrae: 12+15. Gill rakers on the anterior arm of the first arch: 9–10. Branchiostegal rays: 5; Scales lateral series: 24–25.

First pleural rib on parapophysis of first vertebra; parapophysis not reduced; no pleural ribs on hemal spines; hypural plates fused into hypural fan. Epipleural ribs not bifid.

Anal fin not modified into a gonopodium; anal fin musculature unmodified; first proximal radial present; middle anal radials present.

Spermatozeugmata not formed; fertilization external; development nonannual; oviparous. Eggs round.

One dorsal ray articulating with the first two dorsal radials; dorsal fin origin opposite origin of anal.

Autopterotic fossa moderate; lateral ethmoid not expanded medially, not reaching parasphenoid; parasphenoid not expanded anteriorly; no supraoccipital and exoccipital processes; neural arches of first vertebra open, not forming a spine; first vertebra articulates with skull via basioccipital and exoccipital condyles; supraoccipital excluded from formation of foramen magnum; parietals present; nasals not expanded medially. Lateral ethmoid with reduced anterior facet.

Mesethmoid ossified; medial processes of pelvic fin base and ischial process not reduced; interarcual cartilage reduced, attaches laterally to second pharyngobranchial with a bony flange; basihyal long and narrow; no tooth patches on second and third hypobranchials; teeth on fourth ceratobranchials; dorsal hypohyal absent; anterior extension of anterior ceratohyal ventral to ventral hypohyal; uncinate process on fourth epibranchial articulates with that of third; first epibranchial wide at its base; interhyal ossified; two ossified basibranchials. Vomer with posterior extension ventral to parasphenoid.

Lacrimal flat and broad, carrying a distinct sensory canal; dermosphenotic and preopercular with distinct sensory canal; pectoral girdle lowset; first postcleithrum present; posttemporal with ossified lower limb; posttemporal not fused to supracleithrum.

Vomer ossified, edentulous; medial arm of maxilla twisted with no pronounced dorsal process; ventral arms projecting anteriorly with pronounced hooks, not abutting rostral cartilage; outer arm narrow.

Premaxillary ascending processes narrow and elongate, not tapered posteriorly and not overlapping in the midline; rostral cartilage reduced; outer arm of premaxilla with alveolar process, indented posteriorly to form S-shaped arm; No ligament from the ventral arms of maxillaries to middle of rostral cartilage; no ethmomaxillary ligament; no meniscus between premaxilla and maxilla. Unicuspid bi- or tri-serial outer teeth.

Dentary expanded medially, robust; coronoid process on dentary not overlapping with that of articular; retroarticular not elongate. Autopalatine with head angled anteriorly; ventral process elongate reaching quadrate; metapterygoid absent.

Orbital rim free; anterior naris not tubular; supraorbital sensory pores 6–7; seven preopercular pores; four mandibular pores; three lacrimal pores.

Females larger than males; males never with fin extensions; body form quadrangular; series of silvery crossbars on sides of body.

No fatty predorsal ridge; swimbladder does not extend posteriorly beyond hemal spines.

DISTRIBUTION: Brackish water from Florida to Texas.

MATERIAL EXAMINED: *A. multifasciata*: Louisiana: USNM 124795 (2*/33); *A. xenica*: Alabama: AMNH 35673 (2*/19).

### DIVISION 2

DIAGNOSIS: Distinguished from all other cyprinodontiforms by two derived characters: maxilla with a straight proximal arm; and an enlarged dorsal process of the maxilla.

### SEPT 1

### FAMILY VALENCIIDAE, NEW FAMILY

Type Genus *Valencia* Myers 1928b.

DIAGNOSIS: Distinguished from all other cyprinodontiforms by an elongate and attenuate dorsal process of the maxilla.

COMPOSITION: One genus, *Valencia,* and two nominal species: *hispanica* (Cuvier and Valenciennes) and *letourneauxi* (Sauvage).

DISTRIBUTION: Fresh waters of southeastern Spain, Italy, and Corfu.

### GENUS *VALENCIA* MYERS

*Valencia* Myers, 1928b, p. 8 (type species *Hydrargyra hispanica* Cuvier and Valenciennes, by original designation).

ETYMOLOGY: *Valencia* to connote the occurrence of the genus in Valencia, Spain.

COMPOSITION: As for the family.

DIAGNOSIS: As for the family.

DEFINITION: Anal: i, 13; Dorsal: i, 9; Pelvic: 6; Pectoral: 15; Caudal: 8, 19, 8; Vertebrae: 13+16; Gill rakers on the anterior arm of the first arch: 12–13; Branchiostegal rays: 6; Scales lateral series: 28.

First pleural rib on parapophysis of second vertebra; parapophysis not reduced; no pleural ribs on hemal spines; hypural plates fused into hypural fan. Epipleural ribs not bifid.

Anal fin not modified into a gonopodium; anal fin musculature unmodified; first proximal radial present; middle anal radials present.

Spermatozeugmata not formed; fertilization external; development nonannual; oviparous. Eggs round.

One dorsal ray articulating with the first two dorsal radials; dorsal fin origin opposite origin of anal.

Autopterotic fossa moderate; lateral ethmoid not expanded medially, not reaching parasphenoid; parasphenoid not expanded anteriorly; weakly formed supraoccipital and exoccipital processes; neural arches of first vertebra open, not forming a spine; first vertebra articulates with skull via basioccipital and exoccipital condyles; supraoccipital excluded from formation of foramen magnum; parietals present; nasals not expanded medially. Lateral ethmoid with reduced anterior facet.

Mesethmoid ossified; medial processes of pelvic fin base and ischial process not reduced; interarcual cartilage reduced, attaches laterally to second pharyngobranchial with a bony flange; basihyal long and narrow; no tooth patches on second and third hypobranchials; teeth on fourth ceratobranchials; dorsal hypohyal absent; anterior extension of anterior ceratohyal ventral to ventral hypohyal; uncinate process on fourth epibranchial articulates with that of third; first epibranchial wide at its base; interhyal ossified; two ossified basibranchials. Vomer with posterior extension ventral to parasphenoid.

Lacrimal flat and broad, carrying a distinct sensory canal; dermosphenotic and preopercular with distinct sensory canal; pectoral girdle lowset; first postcleithrum present; posttemporal with ossified lower limb; posttemporal not fused to supracleithrum.

Vomer ossified, edentulous; medial arm of maxilla straight with elongate dorsal process; ventral arms not abutting rostral cartilage; outer arm narrow.

Premaxillary ascending processes narrow and elongate, not tapered posteriorly and not overlapping in the midline; rostral cartilage reduced; outer arm of premaxilla with alveolar process, indented posteriorly to form S-shaped arm. No ligament from the ventral arms of maxillaries to middle of rostral cartilage; no ethmomaxillary ligament; no meniscus between premaxilla and maxilla. Unicuspid bi- or tri-serial outer teeth.

Dentary expanded medially, robust; coronoid process on dentary not overlapping with that of articular; retroarticular not elongate. Autopalatine with head angled anteriorly; ventral process elongate reaching quadrate; metapterygoid absent.

Orbital rim free; anterior naris not tubular; supraorbital sensory pores 1–2a, 2b–4a, 4b–7; seven preopercular pores; four mandibular pores; three lacrimal pores.

Females larger than males; males with enlarged dorsal and anal fins; pigmentation pattern consisting of a series of medium brown reticulations on the unpaired fins.

No fatty predorsal ridge; swimbladder does not extend posteriorly beyond hemal spines.

DISTRIBUTION: As for the family.

REMARKS: The genus *Valencia* has been confused with both *Fundulus* and *Aphanius*, the former on the basis of shared primitive characters and the latter on its distribution. *Valencia* is not closely related to the other Old World Laurasian cyprinodonts, and its similarities to the fundulines have been shown to be derived for a much larger group.

MATERIAL EXAMINED: Spain: *V. hispanica*: AMNH 38401 2*/5; Italy: ANSP 7254 (1); Corfu: *Fundulus letourneauxi*: Syntypes BMNH 1880.9.13:1–6 (4).

### SEPT 2

DIAGNOSIS: Distinguished from all other cyprinodontiforms by three derived characters: ascending processes of the premaxillaries short and narrow; dorsal processes of the maxillaries rounded or greatly reduced; and nasals expanded medially.

### SUPERFAMILY POECILIOIDEA

DIAGNOSIS: Distinguished from other cyprinodontiform fishes by the following derived characters: maxilla with an expanded distal arm; parasphenoid with expanded anterior arm; dorsal processes of the maxillaries with a distinct lateral indentation; primitively an elongate retroarticular and a pouch created by scales surrounding the urogenital opening of females.

### FAMILY ANABLEPIDAE GARMAN

Type Genus *Anableps* (Gronow) Scopoli, 1777.

DIAGNOSIS: Distinguished from all other fishes of the order Cyprinodontiformes by robust epiotic and supraoccipital processes; and an outer row of tricuspidate teeth, at least in juveniles or embryos, and several inner rows of unicuspidate or tricuspidate jaw teeth.

COMPOSITION: Three genera: *Anableps* (Gronow) Scopoli, three species: *dowi* Gill, *anableps* Linnaeus, and *microlepis* Müller and Troschel; *Oxyzygonectes* Fowler, with one species: *dowi* (Günther); and *Jenynsia* Günther, with four species: *lineata* (Günther), *eigenmanni* (Haseman), *maculata* (Regan) and *pygogramma* (Boulenger).

DISTRIBUTION: Southern Mexico to Nicaragua; northern coast of South America from Venezuela to Para, Brazil; southern South America (southern Brazil, Argentina, Uruguay) (fig. 78).

### SUBFAMILY ANABLEPINAE GARMAN

DIAGNOSIS: Distinguished from all other cyprinodontiforms by having thickened and elongated anal rays in males which are twisted around each other and covered by a fleshy tube, tubular sperm duct, gonopodium offset either to the left or to the right, proximal anal radials enlarged and derived pigmentation pattern.

COMPOSITION: Two genera, *Anableps* and *Jenynsia* with species as listed for the family.

DISTRIBUTION: As for the family.

### GENUS *ANABLEPS* (GRONOW) SCOPOLI

*Anableps* (Gronow) Scopoli, 1777, p. 450 (type species *Anableps anableps* Linnaeus, by original designation).

*Peltatetrops* Fowler, 1931, p. 396 (type species *Anableps microlepis* Müller and Troschel, by original designation [proposed as a subgenus]).

ETYMOLOGY: *Anableps* from the Greek *ana*, meaning great or enlarged and *bleps*, meaning eye referring to the enlarged orbits of this genus.

COMPOSITION: Three species as listed for the family.

DIAGNOSIS: Distinguished from all other cyprinodontiform fishes by enlarged supraorbital processes of the frontals to accommodate enlarged eyes divided horizontally to effect vision above and below the water; vertebrae 45 or more; posterior section or supraorbital sensory pore pattern represented by pores 6 and 7 only; head scales arranged in random pattern; gonopodium formed principally from anal rays 3 through 9; upper jaw blunt with a reduced premaxillary ascending processes; dumbbell-shaped rostral cartilage; and from *Jenynsia* and *Oxyzygonectes* by possessing a tubular anterior naris; and enlarged pectoral fins with 20 rays or more.

DEFINITION: Anal: (ii) 9–10; Dorsal: 7–10; Pelvic: 6; Pectoral: 20–26; Caudal: 6, 16, 6; Vertebrae: 45–54; Gill rakers on the anterior arm of the first arch: 21–30; Branchiostegal rays: 6; Scales lateral series: 50–96.

First pleural rib on parapophysis of second vertebra; parapophysis not reduced; no pleural ribs on hemal spines; hypural plates fused into hypural fan. Epipleural ribs not bifid.

Anal fin modified into a gonopodium formed principally from anal rays 3 through 9; anal fin musculature unmodified; proximal anal radials expanded and positioned anteriorly; middle anal radials present; sexual dextrality: males with gonopodium offset to the left or the right; females with one or two scales covering left or right side of urogenital opening; gonopodium scaled; tubular sperm duct opening at tip of gonopodium.

Spermatozeugmata in some species; fertilization internal; viviparous; intrafollicular gestation.

One dorsal ray articulating with the first two dorsal radials; dorsal fin set back on posterior third of body.

Autopterotic fossa moderate; lateral ethmoid not expanded medially, not reaching parasphenoid; parasphenoid expanded anteriorly; enlarged supraoccipital and exoccipital processes; neural arches of first vertebra open, not forming a spine; first vertebra articulates with skull via basioccipital and exoccipital condyles; supraoccipital excluded from formation of foramen magnum; parietals present; nasals reduced; supraorbital processes of frontal expanded to accommodate enlarged eyes possessing divided retinas.

Mesethmoid ossified; medial processes of pelvic fin base and ischial process not reduced; interarcual cartilage reduced, attaches laterally to second pharyngobranchial toothplate with a bony flange; basihyal long and narrow; tooth patches on second and third hypobranchials; teeth on fourth ceratobranchials; dorsal hypohyal absent; anterior extension of anterior ceratohyal ventral to ventral hypohyal; uncinate process on fourth epibranchial articulates with that of third; first epibranchial wide at its base; interhyal ossified; two ossified basibranchials. Vomer with posterior extension ventral to parasphenoid.

Lacrimal flat and broad, carrying a distinct sensory canal; dermosphenotic and preopercular with distinct sensory canal; pectoral girdle lowset; first postcleithrum present or absent; posttemporal with ossified lower limb; posttemporal not fused to supracleithrum.

Vomer ossified, edentulous; medial arm of maxilla straight with pronounced dorsal process indented laterally; ventral arms not abutting rostral cartilage; outer arm spatulate.

Premaxillary ascending processes narrow and reduced, not tapered posteriorly and not overlapping in the midline; dumbbell shaped rostral cartilage; outer arm of premaxilla with alveolar process, indented posteriorly to form S-shaped arm. No ligament from the ventral arms of maxillaries to middle of rostral cartilage; no ethmomaxillary ligament; no meniscus between premaxilla and maxilla. Weakly tricuspid outer teeth.

Dentary expanded medially, robust; coronoid process on dentary not overlapping with that of articular; retroarticular elongate. Autopalatine with head angled anteriorly; ventral process elongate reaching quadrate; metapterygoid absent.

Orbital rim free; anterior naris tubular; supraorbital sensory pores 1–2, 3–4a, 6–7; seven preopercular pores; four mandibular pores; two to four lacrimal pores.

Females larger than males; males never with fin extensions; lower rays of caudal drawn into a lobe in one species (*microlepis*); pigmentation pattern consisting of longitudinal stripes of varying number and width.

No fatty predorsal ridge; swimbladder does not extend posteriorly beyond hemal spines.

DISTRIBUTION: Central America, both Atlantic and Pacific slopes; northern South America.

REMARKS: The genus has been most recently reviewed by Miller (1979); Grier, Burns and Flores (MS) described the formation of spermatozeugmata in *A. dowi*. Ranges of meristic characters are supplemented by data from Miller (1979).

MATERIAL EXAMINED: *A. dowi*: Guatemala: Santa Rosa: AMNH 32449 (30); AMNH 24402 (12); Jutiapa: AMNH 31529 (25); No data: AMNH 20830 (2*); AMNH 38412SW (1+).

### GENUS *JENYNSIA* GÜNTHER

*Jenynsia* Günther, 1866, p. 331 (type species *Lebias lineata* Jenyns, by original designation).
*Fitzroyia* Günther, 1866, p. 307 (type species *Lebias multidentata* Jenyns, by original designation).

ETYMOLOGY: *Jenynsia,* a patronym for Jenyns, author of the "Fish Section" of the *Voyage of the Beagle. Fitzroyia* and *Jenynsia* were proposed in the same work by Günther, and although *Fitzroyia* has page priority, the name *Jenynsia* should be used since it was accepted by earlier writers who regarded the two genera as synonyms.

TYPES: South America (Voyage of the Beagle): *Lebias lineata* Jenyns, Types: BMNH 1917.7.14.20–23.

COMPOSITION: Four species as listed for the family.

DIAGNOSIS: Distinguished from all other cyprinodontiforms by tricuspidate outer jaw teeth in adults; an unscaled gonopodium formed principally from rays 3, 6, and 7; and an enlarged sixth middle anal radial.

DEFINITION: Anal: ii, 8; Dorsal: i, 8; Pelvic: 6; Pectoral: 15; Caudal: 8, 17, 8; Vertebrae: 13+16. Gill rakers on the anterior arm of the first arch: 10–11. Branchiostegal rays: 5; Scales lateral series: 25–28.

First pleural rib on parapophysis of second vertebra; parapophysis not reduced; no pleural ribs on hemal spines; hypural plates fused into hypural fan. Epipleural ribs not bifid.

Anal fin modified into a gonopodium formed principally from anal rays 3, 6, and 7; anal musculature unmodified; first proximal radial present; middle anal radials present, sixth enlarged in both males and females; gonopodium unscaled; tubular sperm duct opening at tip of gonopodium.

Spermatozeugmata not formed; fertilization internal; viviparous; intraovarian gestation.

One dorsal ray articulating with the first two dorsal radials; dorsal fin origin opposite origin of anal.

Autopterotic fossa moderate; lateral ethmoid not expanded medially, not reaching parasphenoid; parasphenoid expanded anteriorly; enlarged supraoccipital and exoccipital processes; neural arches of first vertebra open, not forming a spine; first vertebra articulates with skull via basioccipital and exoccipital condyles; supraoccipital excluded from formation of foramen magnum; parietals present; nasals expanded medially.

Mesethmoid ossified; medial processes of pelvic fin base and ischial process not reduced; interarcual cartilage reduced, attaches laterally to second pharyngobranchial with a bony flange; basihyal long and narrow; no tooth patches on second and third hypobranchials; teeth on fourth ceratobranchials; dorsal hypohyal absent; anterior extension of anterior ceratohyal ventral to ventral hypohyal; uncinate process on fourth epibranchial articulates with that of third; first epibranchial wide at its base; interhyal ossified; two ossified basibranchials. Vomer with posterior extension ventral to parasphenoid.

Lacrimal flat and broad, carrying a distinct sensory canal; dermosphenotic and preopercular with distinct sensory canal; pectoral girdle lowset; first postcleithrum present; posttemporal with ossified lower limb; posttemporal not fused to supracleithrum.

Vomer ossified, edentulous; medial arm of maxilla straight with pronounced dorsal process indented laterally; ventral arms narrow, not abutting rostral cartilage; outer spatulate.

Premaxillary ascending processes narrow and reduced, not tapered posteriorly and not overlapping in the midline; rostral cartilage reduced; outer arm of premaxilla with alveolar process, indented posteriorly to form S-shaped arm; No ligament from the ventral arms of maxillaries to middle of rostral cartilage; no ethmomaxillary ligament; no meniscus between premaxilla and maxilla. Tricuspid bi- or tri-serial outer teeth.

Dentary expanded medially, robust; coronoid process on dentary not overlapping with that of articular; retroarticular elongate. Autopalatine with head angled anteriorly; ventral process elongate reaching quadrate; metapterygoid absent.

Orbital rim free; anterior naris not tubular; supraorbital sensory pores 1–2a, 2b–4a, 4b–7; seven preopercular pores; four mandibular pores; three lacrimal pores.

Females larger than males; males never with fin extensions. Pigmentation pattern consisting of dark interrupted stripes.

No fatty predorsal ridge; swimbladder does not extend posteriorly beyond hemal spines.

DISTRIBUTION: Southern South America: lowlands of Brazil, Paraguay, Uruguay, and Argentina.

REMARKS: The genus *Jenynsia* has been confused in past classifications with the cyprinodontines since both possess tricuspidate outer teeth. The variability in the size and shape of these teeth in *Jenynsia* indicates that dental morphological data should be used with caution in a phylogenetic study, especially when there are ontogenetic changes in tooth structure as in *Anableps* and *Oxyzygonectes*.

MATERIAL EXAMINED: *J. lineata*: the types as listed above; Brazil: CAS 40706 (4*/62); AMNH 12938 (1+/2); *J. pygogramma*: Cordova: Types: BMNH 1902. 5. 22. 72–81 (4): *J. maculata*: Argentina: Salta: Types: BMNH 1906. 5.31. 62–71 (9); sp.: Brazil: Santa Catarina, Rio Pique: USNM uncat. (Field no. SW 9-22-77 -3) (6); Lago Perto do mar: USNM uncat. (Field no. SW 9-19-77-1) (7).

## SUBFAMILY OXYZYGONECTINAE, NEW SUBFAMILY

TYPE GENUS: *Oxyzygonectes* Fowler, 1916

DIAGNOSIS: Distinguished from all other cyprinodontiforms by having an inner series of tricuspidate jaw teeth arranged in four or five closely packed rows; a series of scales overlying the preorbital canal; males with anal papilla and enlarged premaxillary ascending processes.

COMPOSITION: Solely the type.

DISTRIBUTION: Pacific coast of Costa Rica.

## GENUS *OXYZYGONECTES* FOWLER

*Oxyzygonectes* Fowler, 1916, p. 425 (type species *Haplochilus dovii* Günther, by original designation [proposed as a subgenus]).

ETYMOLOGY: *Oxyzygonectes,* after the Greek *oxy,* meaning pointed and *Zygonectes,* a presumed close relative in reference to the pointed snout. Miller (1966) has shown that the specific modifier should be *dowi,* not *dovii* or *dovi* since the name is a patronym for Capt. J. M. Dow.

TYPES: Costa Rica: Punta Arena: *Haplochilus dovii* Günther, Types BMNH. 1865.7.20 29–30 (2).

COMPOSITION: Solely the type.

DIAGNOSIS: As for the subfamily above.

DEFINITION: Anal: ii, 10; Dorsal: i, 6; Pelvic: 6; Pectoral: 16–17; Caudal: 7, 15, 7; Vertebrae: 13+15; Gill rakers on the anterior arm of the first arch: 15–16. Branchiostegal rays: 6; Scales lateral series: 29–30.

First pleural rib on parapophysis of second vertebra; parapophysis not reduced; no pleural ribs on hemal spines; hypural plates fused into hypural fan; Epipleural ribs not bifid.

Anal fin not modified into a gonopodium; anal fin musculature unmodified; first proximal radial present; middle anal radials present.

Spermatozeugmata not formed; fertilization external; development nonannual; oviparous. Eggs round.

One dorsal ray articulating with the first two dorsal radials; dorsal fin origin posterior to origin of anal.

Autopterotic fossa moderate; lateral ethmoid slightly expanded medially, not reaching parasphenoid; parasphenoid expanded anteriorly; enlarged supraoccipital and exoccipital processes; neural arches of first vertebra open, not forming a spine; first vertebra articulates with skull via basioccipital and exoccipital condyles; supraoccipital excluded from formation of foramen magnum; parietals present; nasals expanded medially.

Mesethmoid ossified; medial processes of pelvic fin base and ischial process not reduced; interarcual cartilage reduced, attaches laterally to second pharyngobranchial toothplate with a bony flange; basihyal long and narrow; tooth patches on second and third hypobranchials; teeth on fourth ceratobranchials; dorsal hypohyal absent; anterior extension of anterior ceratohyal ventral to ventral hypohyal; uncinate process on fourth epibranchial articulates with that of third; first epibranchial wide at its base; interhyal ossified; two ossified basibranchials. Vomer with posterior extension ventral to parasphenoid.

Lacrimal flat and broad, carrying a distinct sensory canal; dermosphenotic and preopercular with distinct sensory canal; pectoral girdle lowset; first postcleithrum present; posttemporal with ossified lower limb; posttemporal not fused to supracleithrum.

Vomer ossified, edentulous; medial arm of maxilla straight with pronounced dorsal process indented laterally; ventral arms narrow, not abutting rostral cartilage; outer arm spatulate.

Premaxillary ascending processes narrow and reduced, not tapered posteriorly and not overlapping in the midline; rostral cartilage absent; outer arm of premaxilla with alveolar process, indented posteriorly to form S-shaped arm; no ligament from the ventral arms of maxillaries to middle of rostral cartilage; no ethmomaxillary ligament; no meniscus between premaxilla and maxilla. Weakly tricuspid outer row of outer teeth. Several inner rows of closely packed tricuspid teeth.

Dentary expanded medially, robust; coronoid process on dentary not overlapping with that of articular; retroarticular elongate. Autopalatine with head angled anteriorly; ventral process elongate reaching quadrate; metapterygoid absent.

Orbital rim free; anterior naris not tubular; supraorbital sensory pores 1–2a, 2b–4a, 4b–7; seven preopercular pores; four mandibular pores; three lacrimal pores.

Females larger than males; middle rays of caudal never elongate; no throat bars present.

Males and females dark brown overall; males with spotted dorsal and anal fins, and several weak crossbars just anterior to the caudal peduncle; females' unpaired fins pale. In life, males with a blue tinge on the dorsal surface, and both males and females with a shiny white spot on dorsal aspect of orbit. Males with urogenital papilla offset to the left or right in preservation; females with scaled, fleshy pouch covering first several anal fin rays.

No fatty predorsal ridge; swimbladder does not extend posteriorly beyond hemal spines.

DISTRIBUTION: As for the subfamily.

REMARKS: The genus *Oxyzygonectes* had previously been placed in the subfamily Fundulinae.

MATERIAL EXAMINED: Costa Rica: the syntypes, as listed above; Golfito: AMNH 17657 (1*/1+/8); AMNH 37733 (2*/25).

### FAMILY POECILIIDAE GARMAN

Type Genus *Poecilia* Bloch and Schneider, 1801.

DIAGNOSIS: Distinguished from all other cyprinodontiforms by the following derived characters: pectoral fins set high on the sides effected by the dorsal placement of the radials; a hyoid bar with no ventral extension of the anterior ceratohyal accompanied by the ventral hypohyal typically forming a bony cap over its anterior facet; pleural ribs on the first several hemal arches; the anterior placement of the pelvic fins and their inferred anterior migration during growth; and recessed supraorbital sensory pores 2b through 4a.

COMPOSITION: Three subfamilies: Poeciliinae Garman, Fluviphylacinae Roberts, and Aplocheilichthyinae Myers, as defined below.

DISTRIBUTION: (fig. 80) North and Middle America, Caribbean, South America to southern Uruguay; Africa (Congo Basin and the African rift lakes); Dar es Salaam and Madagascar.

### SUBFAMILY POECILIINAE GARMAN

DIAGNOSIS: Distinguished from all other cyprinodontiform fishes by the gonopodium of males formed principally from anal rays 3, 4, and 5, enlarged hemal arches providing its support; expanded inclinators of the anal fin to form a fan-shaped mass; pelvic fins of males with curved rays inferred to function during copulation.

COMPOSITION: Approximately 200 species in 16 genera.

DISTRIBUTION: North America through Central America, the Caribbean, through South America to Uruguay.

DEFINITION: Anal: iii, 6; Dorsal: 4–14; Pelvic: 6; Pectoral: 9–16; Caudal: 8, 11, 8–8, 15, 8; Vertebrae: 11+26. Gill rakers on the anterior arm of the first arch: 6–27. Branchiostegal rays: 5; Scales lateral series: 30–34.

First pleural rib on parapophysis of second vertebra; parapophysis not reduced; no pleural ribs on hemal spines; hypural plates fused into hypural fan; Epipleural ribs not bifid.

Anal fin modified into a gonopodium formed principally from anal rays 3, 4, and 5; hemal arches expanded and projecting anteriorly; proximal radials enlarged; anal fin musculature expanded into fan-shaped mass; first proximal radial present; middle anal radials present.

Spermatozeugmata formed; fertilization internal; development nonannual; oviparious, ovoviviparous, viviparous. Gestation intra- or extra-follicular; superfetation occurs in some.

One dorsal ray articulating with the first two dorsal radials; dorsal fin origin opposite origin of anal.

Autopterotic fossa moderate; lateral ethmoid not expanded medially, not reaching parasphenoid; parasphenoid not expanded anteriorly; weakly formed supraoccipital and exoccipital processes; neural arches of first vertebra open and often expanded, not forming a spine; first vertebra articulates with skull via basioccipital condyles; exoccipital condyles absent; supraoccipital excluded from formation of foramen magnum; parietals present or absent; nasals expanded medially.

Mesethmoid ossified; medial processes of pelvic fin base and ischial process not reduced; interarcual cartilage absent or reduced attaching laterally to second pharyngobranchial with a bony flange; basihyal long and narrow; tooth patches on second and third hypobranchials present or absent; teeth on fourth ceratobranchials; dorsal hypohyal absent; anterior extension of anterior ceratohyal reduced or absent; ventral hypohyal expanded; uncinate process on fourth epibranchial articulates with that of third or absent; first epibranchial narrow at its base; interhyal ossified; two ossified basibranchials. Vomer with posterior extension ventral to parasphenoid.

Lacrimal flat and broad, carrying a distinct sensory canal; dermosphenotic and preopercular with distinct sensory canal; pectoral girdle highset; first postcleithrum absent; posttemporal with ossified lower limb; posttemporal not fused to supracleithrum.

Vomer ossified, edentulous; medial arm of maxilla straight with pronounced dorsal process indented laterally; ventral arms not abutting rostral cartilage; outer arm narrow.

Premaxillary ascending processes narrow and reduced, not tapered posteriorly and not overlapping in the midline; rostral cartilage reduced or absent; outer arm of premaxilla with alveolar process, indented posteriorly to form S-shaped arm. No ligament from the ventral arms of maxillaries to middle of rostral cartilage; no ethmomaxillary ligament; no meniscus between premaxilla and maxilla. Unicuspid bi- or tri-serial outer teeth.

Dentary expanded medially, robust; coronoid process on dentary not overlapping with that of articular; retroarticular not elongate. Autopalatine with head angled anteriorly; ventral process elongate reaching quadrate; metapterygoid absent.

Orbital rim free; anterior naris not tubular; supraorbital sensory pores 1–2a, recessed 2b–4a, 4b–7; seven preopercular pores; four mandibular pores; three or four lacrimal pores.

Females larger than males; males often with fin extensions; males drab to elaborately pigmented; females typically drab.

No fatty predorsal ridge; swimbladder does not extend posteriorly beyond hemal spines.

REMARKS: The subfamily Poeciliinae as the term is used here is equivalent to the family Poeciliidae of previous authors.

Ranges for meristic characters are for specimens examined.

MATERIAL EXAMINED: *Tomeurus gracilis*: Aquarium material: AMNH 22685 (16+); *Poecilia vivipara*: Brazil: Rio de Janeiro; AMNH 20708 (5+/20); *Belonesox belizanus maxillosus*: Aquarium material: AMNH 27493SW (5+/5); *Xiphophorus helleri*: Aquarium material: AMNH 38409 (3*/3).

FOSSILS: Upper Tertiary fossil poeciliids are known from Brazil.

### SUBFAMILY APLOCHEILICHTHYINAE MYERS

Type Genus *Aplocheilichthys* Bleeker.

DIAGNOSIS: Distinguished from other poecilioids by the possession of a cartilaginous mesethmoid, and lateral ethmoid expanded toward the parasphenoid.

COMPOSITION: Eight genera in over 100 species: *Aplocheilichthys* Bleeker, "*Aplocheilichthys*," *Lamprichthys* Regan, *Procatopus* Boulenger, *Pantanodon* Myers, *Cynopanchax* Ahl, *Plataplochilus* Ahl and *Hypsopanchax* Myers.

DISTRIBUTION: Savanna and forest lowland regions of central and east Africa south of the Sahara, the Rift lakes, and Madagascar.

### GENUS *APLOCHEILICHTHYS* BLEEKER

*Aplocheilichthys* Bleeker, 1863, p. 116 (type species *Poecilia spliauchena* Dumeril, by monotypy).

*Haplochilichthys* Regan, 1911, p. 323 (emendation of spelling of *Aplocheilichthys* Bleeker).

ETYMOLOGY: *Aplocheilichthys* after *Aplocheilus* McClelland, another cyprinodontiform genus, and *ichthys*, referring to a presumed close relationship between the two genera.

TYPES: *Poecilia spilauchena* Dumeril, BMNH.

DIAGNOSIS: Distinguished from other poecilioid fishes by possessing a first postcleithrum, and from other procatopines by having an unexpanded swimbladder, and an anal fin with less than 14 rays.

DEFINITION: Anal: ii, 10; Dorsal: i, 9; Pelvic: 6; Pectoral: 13–15; Caudal: 6, 14, 6; Vertebrae: 12+13; Gill rakers on the anterior arm of the first arch: 7–8. Branchiostegal rays: 5; Scales lateral series: 28–30.

First pleural rib on parapophysis of second vertebra; parapophysis not reduced; often a pleural rib on hemal spines; hypural plates fused into hypural fan. Epipleural ribs not bifid.

Anal fin not modified into a gonopodium; anal fin musculature unmodified; first proximal radial present; middle anal radials present; urogenital opening of female covered with a pocket of scales.

Spermatozeugmata not formed; fertilization external; development nonannual; oviparous. Eggs round.

One dorsal ray articulating with the first two dorsal radials; dorsal fin origin opposite origin of anal.

Autopterotic fossa moderate; lateral ethmoid expanded medially, reaching parasphenoid; parasphenoid expanded anteriorly; no supraoccipital and exoccipital processes; neural arches of first vertebra open, not forming a spine; first vertebra articulates with skull via basioccipital and exoccipital condyles; supraoccipital excluded from formation of foramen magnum; parietals absent; nasals expanded medially.

Mesethmoid unossified; medial processes of pelvic fin base and ischial process not reduced; interarcual cartilage reduced, attaches laterally to second pharyngobranchial with a bony flange; basihyal long and narrow; no tooth patches on second and third hypobranchials; teeth on fourth ceratobranchials; dorsal hypohyal absent; anterior extension of anterior ceratohyal reduced; ventral hypohyal enlarged; uncinate process on fourth epibranchial articulates with that of third; first epibranchial wide at its base; interhyal ossified; two ossified basibranchials. Vomer with posterior extension ventral to parasphenoid.

Lacrimal flat and broad, carrying a distinct sensory canal; dermosphenotic and preopercular with distinct sensory canal; pectoral girdle highset; first postcleithrum present; posttemporal with ossified lower limb; posttemporal not fused to supracleithrum.

Vomer ossified, edentulous; medial arm of maxilla straight with pronounced dorsal process indented laterally; ventral arms not abutting rostal cartilage; outer arm expanded.

Premaxillary ascending processes narrow and reduced, not tapered posteriorly and not overlapping in the midline; rostral cartilage reduced or absent; outer arm of premaxilla with alveolar process, indented posteriorly to form S-shaped arm. No ligament from the ventral arms of maxillaries to middle of rostral cartilage; no ethmomaxillary ligament; no meniscus between premaxilla and maxilla. Unicuspid bi- or tri-serial outer teeth.

Dentary expanded medially, robust; coronoid process on dentary not overlapping with that of articular; retroarticular elongate. Autopalatine with head angled anteriorly; ventral process elongate reaching quadrate; metapterygoid absent.

Orbital rim free; anterior naris not tubular; supraorbital sensory pores 1–2a, recessed 2b–4a, 4b–7; seven preopercular pores; four mandibular pores; three lacrimal pores.

Males larger than females; males often with extension of pectoral and caudal fins; body straw-colored overall.

No fatty predorsal ridge; swimbladder does not extend posteriorly beyond hemal spines.

DISTRIBUTION: Savanna and forest regions of central and eastern Africa.

REMARKS: The genus *Aplocheilichthys* cannot be defined as a monophyletic group. The more derived members of the genus are placed in the genus group "*Aplocheilichthys.*" This decision is made here since a revision of the entire genus is necessary to define its major monophyletic subgroups. The following named taxa are treated as subgenera in this analysis:

### SUBGENUS *MICROPANCHAX* MYERS

*Micropanchax* Myers, 1924a, p. 42 (type species *Haplochilus schoelleri* Boulenger, by original designation).

### SUBGENUS *LACUSTRICOLA* MYERS

*Lacustricola* Myers, 1924b, p. 43 (type species *Haplochilus pumilus* Boulenger, by original designation [proposed as a subgenus]).

### SUBGENUS *POROPANCHAX* CLAUSEN

*Poropanchax* Clausen, 1967, p. 12 (type species, *Aplocheilichthys macrophthalmus* Meinken, by original designation).

### SUBGENUS *CONGOPANCHAX* POLL

*Congopanchax* Poll, 1971, p. 303 (type species *Aplocheilichthys myersi* Poll, by original designation).

MATERIAL EXAMINED: *A. spilauchena*: the types as listed above; Ghana: SU 63440 (2*/25); SU 64629 (6); *A. baudoni*: West Africa: AMNH 20936 Paratype (1): *A. pumilus*: Tanganyika: AMNH 8274 (1); Aquarium material: AMNH 27465 (4+); *A. macrophthalmus*: Niger Delta: BMNH 1977. 12.6: 1–10 (1*/10); *A. myersi*: no data: ANSP (2 and young).

### GENUS *LAMPRICHTHYS* REGAN

*Lamprichthys* Regan, 1911, p. 325 (type species *Haplochilus tanganicanus* Boulenger, by original designation).

*Mohanga* Boulenger, 1911, p. 261 (type species *Haplochilus tanganicanus* Boulenger, by original designation).

ETYMOLOGY: *Lamprichthys* from the Latin *lampas*, meaning bright, and *ichthys*, referring to the large, bright eyes typical of procatopines.

TYPES: Lake Tanganyika: *Haplochilus tanganicanus* Boulenger, Type: BMNH 1898.9.9.82 (1).

COMPOSITION: Solely the type species.

DIAGNOSIS: Distinguished from other poecilioids by having up to 41 vertebrae, ctenoid scales, posttemporal with a ligamentous lower limb, and lyre-shaped caudal fin.

DEFINITION: Anal: ii, 26; Dorsal: iii, 13; Pelvic: 6; Pectoral: 17; Caudal: 8, 18, 8; Vertebrae: 14+26–14+27. Gill rakers on the anterior arm of the first arch: 27. Branchiostegal rays: 5; Scales lateral series: 30–33.

First pleural rib on parapophysis of second vertebra; parapophysis not reduced; one or two pleural ribs on hemal spines; hypural plates fused into hypural fan. Epipleural ribs not bifid.

Anal fin not modified into a gonopodium; anal fin musculature unmodified; first proximal radial present; middle anal radials present; urogenital opening of female covered with pocket of scales.

Spermatozeugmata not formed; fertilization external; development nonannual; oviparous. Eggs round.

One dorsal ray articulating with the first two dorsal radials; dorsal fin origin opposite origin of anal.

Autopterotic fossa moderate; lateral ethmoid expanded medially, reaching parasphenoid; parasphenoid expanded anteriorly; weakly formed supraoccipital and exoccipital processes; neural arches of first vertebra open, not forming a spine; first vertebra articulates with skull via basioccipital and exoccipital condyles; supraoccipital excluded from formation of foramen magnum; parietals absent; nasals expanded medially.

Mesethmoid cartilaginous; medial processes of pelvic fin base and ischial process not reduced; interarcual cartilage reduced, attaches laterally to second pharyngobranchial with a bony flange; basihyal long and narrow; no tooth patches on second and third hypobranchials; teeth on fourth ceratobranchials; dorsal hypohyal absent; anterior extension of anterior ceratohyal reduced; ventral hypohyal expanded; uncinate process on fourth epibranchial articulates with that of third; first epibranchial wide at its base; interhyal ossified; two ossified basibranchials. Vomer with posterior extension ventral to parasphenoid.

Lacrimal flat and broad, carrying a distinct sensory canal; dermosphenotic and preopercular with distinct sensory canal; pectoral girdle highset; first postcleithrum absent; posttemporal with unossified lower limb; posttemporal not fused to supracleithrum.

Vomer ossified, edentulous; medial arm of maxilla straight with pronounced dorsal process indented laterally; ventral arms not abutting rostral cartilage; outer arm expanded.

Premaxillary ascending processes narrow and reduced, not tapered posteriorly and not overlapping in the midline; rostral cartilage reduced or absent; outer arm of premaxilla with alveolar process, indented posteriorly to form S-shaped arm. No ligament from the ventral arms of maxillaries to middle of rostral cartilage; no ethmomaxillary ligament; no mensicus between premaxilla and maxilla. Unicuspid bi- or tri-serial outer teeth.

Dentary expanded medially, robust; coronoid process on dentary not overlapping with that of articular; retroarticular not elongate. Autopalatine with head angled anteriorly; ventral process elongate reaching quadrate; metapterygoid absent.

Orbital rim free; anterior naris not tubular; supraorbital sensory pores 1–2a, recessed 2b–4a, 4b–7; seven preopercular pores, four mandibular pores; three lacrimal pores.

Males larger than females; males and females with upper and lower rays of caudal extended; body in life with light blue tinge; color brownish in alcohol.

No fatty predorsal ridge; swimbladder extends posteriorly beyond 12 hemal spines.

DISTRIBUTION: Lake Tanganyika.

MATERIAL EXAMINED: Lake Tanganyika: the types as listed above; FMNH 62958 (1*/4); FMNH 62959 (1*/4); AMNH 11732 (1); AMNH 11728 (2).

## GENUS *PANTANODON* MYERS

*Pantanodon* Myers, 1955, p. 7 (type species *Pantanodon podoxys* Myers, by original designation).

ETYMOLOGY: *Pantanodon* from the Greek *pantos*, meaning all and *anodon*, meaning without teeth referring to the absence of teeth in the jaws in the type species.

TYPES: Dar es Salaam: *Pantanodon podoxys* Myers; Holotype: SU 50194 (1).

COMPOSITION: Two species: *podoxys* Myers and, *madagascariensis* (Arnoult).

DIAGNOSIS: Distinguished from all other cyprinodontiforms by the greatly enlarged second pharyngobranchial toothplate; three pelvic spines in males; the absence of hypobranchials; and from other aplocheilichthyids by the presence of tricuspid inner teeth; the absence of exoccipital condyles; the application of the neurapophyses of the first vertebra to the skull; and an increase in the number of gill rakers on the first arch to 45.

DEFINITION: Anal: iii, 14; Dorsal: i, 8; Pelvic: iii, 3–6; Pectoral: 9; Caudal: 5, 16, 5; Vertebrae: 14+16; Gill rakers on the anterior arm of the first arch: 45; Branchiostegal rays: 5; Scales lateral series: 29–31.

First pleural rib on parapophysis of second vertebra; parapophysis not reduced; no pleural ribs on hemal spines; hypural plates fused into hypural fan. Epipleural ribs not bifid.

Anal fin not modified into a gonopodium; anal fin musculature unmodified; first proximal radial present; middle anal radials present; urogenital opening of female covered with pocket of scales.

Spermatozeugmata not formed; fertilization external; development nonannual; oviparous. Eggs round.

One dorsal ray articulating with the first two dorsal radials; dorsal fin origin opposite origin of anal.

Autopterotic fossa moderate; lateral ethmoid not expanded medially, not reaching parasphenoid; parasphenoid not expanded anteriorly; no supraoccipital and exoccipital processes; neural arches of first vertebra open, not forming a spine; first vertebra articulates with skull via basioccipital condyles; exoccipital condyles absent; supraoccipital excluded from formation of foramen magnum; parietals absent; nasals not expanded medially.

Mesethmoid unossified; medial processes of pelvic fin base and ischial process not reduced; interarcual cartilage absent; second pharyngobranchial toothplate greatly enlarged; basihyal long and narrow; no tooth patches on second and third hypobranchials; teeth on fourth ceratobranchials; dorsal hypohyal absent; anterior extension of anterior ceratohyal reduced; ventral hypohyal expanded; uncinate process on fourth epibranchial; first three epibranchials absent; interhyal ossified; two ossified basibranchials. Vomer with posterior extension ventral to parasphenoid.

Lacrimal narrow, carrying a distinct sensory canal; dermosphenotic and preopercular with distinct sensory canal; pectoral girdle highset; first postcleithrum absent; posttemporal with ossified lower limb; posttemporal not fused to supracleithrum.

Unossified vomer; medial arm of maxilla straight, reduced dorsal process; ventral arms narrow and straight, no abutting rostral cartilage; outer arm narrow.

Premaxillary ascending processes narrow and reduced, not tapered posteriorly and not overlapping in the midline; rostral cartilage reduced or absent; outer arm of premaxilla with alveolar process, indented posteriorly to form S-shaped arm. No ligament from the ventral arms of maxillaries to middle of rostral cartilage; no ethmomaxillary ligament; no meniscus between premaxilla and maxilla. Unicuspid bi- or tri-serial or no outer teeth.

Dentary expanded medially, robust; coronoid process on dentary not overlapping with that of articular; retroarticular not elongate. Autopalatine with head angled anteriorly; ventral process elongate reaching quadrate; metapterygoid absent.

Orbital rim free; anterior naris not tubular; supraorbital sensory pores weakly formed; preopercular canal represented by an open groove.

Males larger than females; males with no fin extensions; caudal fin truncate; body generally straw-colored.

No fatty predorsal ridge; swimbladder extends posteriorly beyond five hemal spines.

DISTRIBUTION: Tanzania, Mozambique, and Madagascar.

REMARKS: The genus *Pantanodon* was placed in its own subfamily, the Pantanodontinae, by Whitehead (1962) on the basis of an absence of teeth in the jaws and other derived specializations of *podoxys*, the only species known at that time.

MATERIAL EXAMINED: *P. podoxys*: Dar es Salaam: the holotype as listed above; paratype: SU 50195 (1); SU 61761; BMNH 1962.4.4.:1–12 (2). *P. madagascariensis*: Paratypes: AMNH 20526 (1*/4).

### GENUS "*APLOCHEILICHTHYS*"

ETYMOLOGY: "*Aplocheilichthys*" is used to reference the more derived species of the genus *Aplocheilichthys*.

COMPOSITION: The more derived species of the genus *Aplocheilichthys* of which *johnstoni* may be considered typical.

DIAGNOSIS: Distinguished from other members of the genus *Aplocheilichthys* and resembling the more derived procatopines by lacking the interarcual cartilage, possessing an unossified vomer, an anal fin of 14 rays or more, swimbladder extending beyond the first three hemal arches, and having a robust lower jaw.

DEFINITION: Anal: iii, 11; Dorsal: ii, 13; Pelvic: 5; Pectoral: 12; Caudal: 6, 9, 6; Vertebrae: 14+16. Gill rakers on the anterior arm of the first arch: 8. Branchiostegal rays: 5; Scales lateral series: 31.

First pleural rib on parapophysis of second vertebra; parapophysis not reduced; one or two pleural ribs on hemal spines; hypural plates fused into hypural fan. Epipleural ribs not bifid.

Anal fin not modified into a gonopodium; anal fin musculature unmodified; first proximal radial present; middle anal radials present; urogenital opening of female covered with pocket of scales.

Spermatozeugmata not formed; fertilization external; development nonannual; oviparous. Eggs round.

One dorsal ray articulating with the first two dorsal radials; dorsal fin origin opposite origin of anal.

Autopterotic fossa moderate; lateral ethmoid expanded medially, reaching parasphenoid; parasphenoid expanded anteriorly; weakly formed supraoccipital and exoccipital processes; neural arches of first vertebra open, not forming a spine; first vertebra articulates with skull via basioccipital and exoccipital condyles; supraoccipital excluded from formation of foramen magnum; parietals absent; nasals expanded medially.

Mesethmoid ossified; medial processes of pelvic fin base and ischial process not reduced; interarcual cartilage absent; second pharyngobranchial possesses a bony flange; basihyal long and narrow; no tooth patches on second and third hypobranchials; teeth on fourth ceratobranchials; dorsal hypohyal absent; anterior extension of anterior ceratohyal reduced; ventral hypohyal expanded, uncinate process on fourth epibranchial articulates with that of third; first epibranchial wide at its base; interhyal ossified; two ossified basibranchials. Vomer with posterior extension ventral to parasphenoid.

Lacrimal flat and broad, carrying a distinct sensory canal; dermosphenotic and preopercular with distinct sensory canal; pectoral girdle highset; first postcleithrum absent; posttemporal with ossified lower limb; posttemporal not fused to supracleithrum.

Vomer ossified, edentulous; medial arm of maxilla straight with pronounced dorsal process indented laterally; ventral arms not abutting rostral cartilage; outer arm expanded.

Premaxillary ascending processes narrow and reduced, not tapered posteriorly and not overlapping in the midline; rostral cartilage reduced or absent; outer arm of premaxilla with alveolar process, indented posteriorly to form S-shaped arm; No ligament from the ventral arms of maxillaries to middle of rostral cartilage; no ethmomaxillary ligament; no meniscus between premaxilla and maxilla. Unicuspid bi- or tri-serial outer teeth.

Dentary expanded medially, extremely robust; coronoid process on dentary not overlapping with that of articular; retroarticular not elongate. Autopalatine with head angled anteriorly; ventral process elongate reaching quadrate; metapterygoid absent.

Orbital rim free; anterior naris not tubular; supraorbital sensory pores 1–2a, recessed 2b–4a, 4b–7; seven preopercular pores; four mandibular pores; three lacrimal pores.

Males larger than females; males and females with truncate caudal fin; body straw-colored overall.

No fatty predorsal ridge; swimbladder extends posteriorly beyond four hemal spines.

DISTRIBUTION: See *Aplocheilichthys* above.

REMARKS: "*Aplocheilichthys*" is not formally named since its limits cannot be readily determined as the genus *Aplocheilichthys* is large (containing over 100 species) and is polyphyletic.

MATERIAL EXAMINED: *A. johnstoni*: No data: ANSP 54348-57 (2*/10).

### GENUS *PROCATOPUS* BOULENGER

*Procatopus* Boulenger, 1904b, p. 20 (type species *Procatopus nototaenia* Boulenger, by original designation).

*Andreasenius* Clausen, 1959, p. 264 (type species *Procatopus aberrans* Ahl, by original designation [proposed as a subgenus]).

*Hylopanchax* Poll and Lambert, 1965, p. 623 (type species *Hypsopanchax silvestris* Poll and Lambert, by original designation).

ETYMOLOGY: *Procatopus* from the Greek *pro,* meaning if front of, *catos,* meaning inferior or ventral, and *op*, meaning opening, referring to the anterior position of the pelvics and anus.

TYPES: Cameroon, Lobi River: *Procatopus nototaenia* Boulenger, Types: BMNH 1904.7.1.141–160.

DIAGNOSIS: Distinguished from all other cyprinodontiforms by having several rays free from the branchiostegal membrane and extending posteriorly in males.

DEFINITION: Anal: (i) 14–17; Dorsal: 7–8; Pelvic: 6; Pectoral: 13; Caudal: 8, 11, 8; Vertebrae: 12+17; Gill rakers on the anterior arm of the first arch: 12–13. Branchiostegal rays: 5; Scales lateral series: 24–28.

First pleural rib on parapophysis of second vertebra; parapophysis not reduced; no pleural ribs on hemal spines; hypural plates fused into hypural fan; Epipleural ribs not bifid.

Anal fin not modified into a gonopodium; anal fin musculature unmodified; first proximal radial present; middle anal radials present; urogenital opening of female covered with pocket of scales.

Spermatozeugmata not formed; fertilization external; development nonannual; oviparous. Eggs round.

One dorsal ray articulating with the first two dorsal radials; dorsal fin origin opposite origin of anal.

Autopterotic fossa moderate; lateral ethmoid expanded medially, reaching parasphenoid; parasphenoid expanded anteriorly; no supraoccipital and exoccipital processes; neural arches of first vertebra open, not forming a spine; first vertebra articulates with skull via basioccipital and exoccipital condyles; supraoccipital excluded from formation of foramen magnum; parietals absent; nasals expanded medially.

Mesethmoid unossified; medial processes of pelvic fin base and ischial process not reduced; interarcual cartilage absent; second pharyngobranchial toothplate possesses a bony flange; basihyal long and narrow; no tooth patches on second and third hypobranchials; teeth on fourth ceratobranchials; dorsal hypohyal absent; anterior extension of anterior ceratohyal reduced; ventral hypohyal expanded; uncinate process on fourth epibranchial articulates with that of third; first epibranchial wide at its base; interhyal ossified; two ossified basibranchials. Vomer with posterior extension ventral to parasphenoid.

Lacrimal flat and broad, carrying a distinct sensory canal; dermosphenotic and preopercular with distinct sensory canal; pectoral girdle highset; first postcleithrum absent; posttemporal with ossified lower limb; posttemporal not fused to supracleithrum.

Unossified vomer; medial arm of maxilla pronounced dorsal process indented laterally; ventral arms narrow and straight, not abutting rostral cartilage; outer arm reduced.

Premaxillary ascending processes narrow and reduced, not tapered posteriorly and not overlapping in the midline; rostral cartilage reduced or absent; outer arm of premaxilla with alveolar process, indented posteriorly to form S-shaped arm. No ligament from the ventral arms of maxillaries to middle of rostral cartilage; no ethmomaxillary ligament; no meniscus between premaxilla and maxilla. Unicuspid bi- or tri-serial outer teeth.

Dentary expanded medially, extremely robust; coronoid process on dentary not overlapping with that of articular; retroarticular not elongate. Autopalatine with head angled anteriorly; ventral process elongate reaching quadrate; metapterygoid absent.

Orbital rim free; anterior naris not tubular; supraorbital sensory pores 1–2a, recessed 2b–4a, 4b–7; seven preopercular pores; four mandibular pores; three lacrimal pores.

Males larger than females; often with caudal fin extensions; one or two branchiostegal rays free from opercular membrane and projecting posteriorly.

No fatty predorsal ridge; swimbladder does not extend posteriorly beyond hemal spines.

DISTRIBUTION: Congo Basin.

REMARKS: The anterior displacement of the pelvic fins has been demonstrated in the genus *Procatopus* (Trewavas, 1974).

MATERIAL EXAMINED: *P. nototaenia*: Cameroon: the types as listed above; SU 47714 (1*/8). *P. gracilis*: Aquarium material: AMNH 38406 (2*/2). *P. silvestris*: Zaire (Congo): UMMZ 188727 (1*/4).

## GENUS *CYNOPANCHAX* MYERS

*Cynopanchax* Ahl, 1928, p. 115 (type species *Haplochilichthys bukobanus* Ahl, by original designation).

ETYMOLOGY: *Cynopanchax* from the Greek *cyno,* meaning dog and *Panchax,* a commonly used generic reference for all Old World cyprinodonts, referring to the presence of an outer row of enlarged, recurved teeth.

COMPOSITION: Solely the type species.

## GENUS *PLATAPLOCHILUS* AHL

*Plataplochilus* Ahl, 1928, p. 116 (type species *Haplochilichthys ngaensis* Ahl, by original designation).

ETYMOLOGY: The genus *Plataplochilus* from the Greek *platys* meaning flat and *Haplochilus,* a general reference for African cyprinodonts, referring to the species as a cyprinodont with a laterally compressed body form.

COMPOSITION: Solely for the type species.

REMARKS: Specimens of *Cynopanchax bukobanus* and *Plataplochilus ngaensis* have not been examined. Ahl (1928) separated the species from other *Aplocheilichthys* species placing them in monotypic genera on the basis of dental characteristics. *Cynopanchax* possesses an outer row of greatly enlarged teeth in the jaws, the lateral pair suggesting canines and therefore the characteristic on which the genus was named. However, from the description, *bukobanus* seems to differ little from primitive *Aplocheilichthys* species. The nonmonophyletic nature of the latter genus does not help in placing *Cynopanchax* or *Plataplochilus* in synonymy of any recognized genus. Lambert and Clausen (1967) redefined *Plataplochilus* using a series of primitive and derived characters none of which was unique. Therefore, the genera are listed here as available generic categories whose membership may be expanded after a revision of the genus *Aplocheilichthys.* Both Myers (1938) and Clausen (1967) were unable to treat these genera in their reviews of the procatopines because of the unavailability of material.

## GENUS *HYPSOPANCHAX* MYERS

*Hypsopanchax* Myers, 1924a, p. 41 (type species *Hypsopanchax platysternus* Myers, by original designation).

*Platypanchax* Ahl, 1928, p. 116 (type species *Haplochilus modestus* Pappenheim, by original designation).

ETYMOLOGY: *Hypsopanchax,* from the Greek *hypso* meaning deep and *Panchax,* a common generic reference for Old World cyprinodonts, referring to the deep body.

TYPES: Zaire (Congo): *Hypsopanchax platysternus* Myers, Type: AMNH 6299 (1).

COMPOSITION: Approximately 15 species as listed in Lazara (1979).

DIAGNOSIS: Distinguished from all other aplocheilichthyids by being deep-bodied as a result of expanded pleural ribs.

DEFINITION: Anal: (ii) 15–19; Dorsal: 12–16; Pelvic: 6; Pectoral: 16; Caudal: 8, 16, 8; Vertebrae: 12+16; Gill rakers on the anterior arm of the first arch: 11–12. Branchiostegal rays: 5; Scales lateral series: 29–30.

First pleural rib on parapophysis of second vertebra; parapophysis not reduced; often a pleural rib on hemal spines; pleural ribs expanded ventrally; hypural plates fused into hypural fan. Epipleural ribs not bifid.

Anal fin not modified into a gonopodium; anal fin musculature unmodified; first proximal radial present; middle anal radials present; urogenital opening of female covered with pocket of scales.

Spermatozeugmata not formed; fertilization external; development nonannual; oviparous. Eggs round.

One dorsal ray articulating with the first two dorsal radials; dorsal fin origin opposite origin of anal.

Autopterotic fossa moderate; lateral ethmoid expanded medially, reaching parasphenoid; parasphenoid expanded anteriorly; no supraoccipital and exoccipital processes; neural arches of first vertebra open, not forming a spine; first vertebra articulates with skull via basioccipital and exoccipital condyles; supraoccipital excluded from formation of foramen magnum; parietals absent; nasals expanded medially.

Mesethmoid unossifed; processes of pelvic fin base and ischial process not reduced; interarcual cartilage absent, second pharyngobranchial toothplate possesses a bony flange; basihyal long and narrow; no tooth patches on second and third hypobranchials; teeth on fourth ceratobranchials; dorsal hypohyal absent; anterior extension of anterior ceratohyal reduced; ventral hypohyal expanded; uncinate process on fourth epibranchial articulates with that of third; first epibranchial wide at its base; interhyal ossified; two ossified basibranchials. Vomer with posterior extension ventral to parasphenoid.

Lacrimal flat and broad, carrying a distinct sensory canal; dermosphenotic and preopercular with distinct sensory canal; pectoral girdle highset; first postcleithrum absent; posttemporal with ossified lower limb; posttemporal not fused to supracleithrum.

Ossified or unossified vomer; medial arm of maxilla pronounced, dorsal process indented laterally; ventral arms narrow and straight, not abutting rostral cartilage; outer arm reduced.

Premaxillary ascending processes narrow and reduced, not tapered posteriorly and not overlapping in the midline; rostral cartilage reduced; outer arm of premaxilla with alveolar process, indented posteriorly to form S-shaped arm. No ligament from the ventral arms of maxillaries to middle of rostral cartilage; no ethmomaxillary ligament; no meniscus between premaxilla and maxilla. Unicuspid bi- or tri-serial outer teeth.

Dentary expanded medially, very robust; coronoid process on dentary not overlapping with that of articular; retroarticular not elongate. Autopalatine with head angled anteriorly; ventral process elongate reaching quadrate; metapterygoid absent.

Orbital rim free; anterior naris not tubular; supraorbital sensory pores 1–2a, recessed 2b–4a, 4b–7; seven preopercular pores; four mandibular and three lacrimal pores.

Males larger than females; caudal fin truncate; pigmentation pattern often consisting of several dark crossbars.

No fatty predorsal ridge; swimbladder extends posteriorly beyond three or four hemal spines.

Distribution: Congo Basin.

Remarks: The genus has been recently reviewed by Poll and Lambert (1965).

Material Examined: *H. platysternus*: Zaire (Congo): the types as listed above; paratypes: AMNH 6078 (1*/12). *H. zebra*: West Africa: Cotype: USNM 92965 (1); USNM 191521 (1*/22). *H. deprimozi*: Congo: SU 17480 (6); BMNH 1974.9.18:522–527.

## SUBFAMILY FLUVIPHYLACINAE ROBERTS

Type Genus *Fluviphylax* Whitley, 1965.

Diagnosis: Diminutive species of the family Poeciliidae distinguished from all other cyprinodontiforms by extremely large eyes and reduced preorbital distance.

Composition: One genus and species: *Fluviphylax pygmaeus* (Myers and Carvalho).

Distribution: Brazil: Amazon Basin.

### GENUS *FLUVIPHYLAX* WHITLEY

*Potamophylax* Myers and Carvalho, in Myers, 1955, p. 7 (type species *Potamophylax pygmaeus* Myers and Carvalho, by original designation [name preoccupied in the Insecta]).

*Fluviphylax* Whitley, 1965, p. 25 (type species *Potamophylax pygmaeus* Myers and Carvalho, by monotypy).

Etymology: *Fluviphylax* from the Latin *fluvius*, meaning a stream or river, and from the Greek *phylax*, meaning a guarder.

Types: Brazil: Rio Madeira at Borba: *Potamophylax pygmaeus* Myers and Carvalho, Paratypes SU 50196 (3).

Composition: As for the subfamily.

Diagnosis: As for the subfamily.

Definition: Anal: ii, 6; Dorsal: 5–6; Pelvic: 6; Pectoral: 10–11; Caudal; 4, 10, 4; Vertebrae: 12+14, 13+13; Gill rakers on the anterior arm of the first arch: 9–10. Branchiostegal rays: 5; Scales lateral series: 24–26.

First pleural rib on parapophysis of second vertebra; parapophysis not reduced; no pleural ribs on hemal spines; hypural plates fused into hypural fan. Epipleural ribs not bifid.

Anal fin not modified into a gonopodium; anal fin musculature unmodified; first proximal radial present; middle anal radials present; urogenital opening of female covered with pocket of scales.

Spermatozeugmata not formed; fertilization external; development nonannual; oviparous. Eggs round.

One dorsal ray articulating with the first two dorsal radials; dorsal fin origin on posterior third of body.

Autopterotic fossa moderate; lateral ethmoid not expanded medially, not reaching parasphenoid; parasphenoid not expanded anteriorly; no supraoccipital and exoccipital processes; neural arches of first vertebra open, not forming a spine; first vertebra articulates with skull via basioccipital and exoccipital condyles; supraoccipital excluded from formation of foramen magnum; parietals absent; nasals expanded medially.

Mesethmoid ossified; medial processes of pelvic fin base and ischial process not reduced; interarcual cartilage reduced, attaches laterally to second pharyngobranchial with a bony flange; basihyal long and narrow; no tooth patches on second and third hypobranchials; teeth on fourth ceratobranchials; dorsal hypohyal absent; anterior extension of anterior ceratohyal reduced; ventral hypohyal expanded; uncinate process on fourth epibranchial articulates with that of third; first epibranchial wide at its base; interhyal ossified; two ossified basibranchials. Vomer with posterior extension ventral to parasphenoid.

Lacrimal reduced, carrying a distinct sensory canal; dermosphenotic and preopercular with distinct sensory canal; pectoral girdle highset; first postcleithrum absent; posttemporal with ossified lower limb; posttemporal not fused to supracleithrum.

Unossified vomer; medial arm of maxilla straight with reduced dorsal process; ventral arms narrow and straight, not abutting rostral cartilage; outer arm narrow.

Premaxillary ascending processes narrow and reduced, not tapered posteriorly and not overlapping in the midline; rostral cartilage reduced; outer arm of premaxilla with alveolar process, indented posteriorly to form S-shaped arm No ligament from the ventral arms of maxillaries to middle of rostral cartilage; no ethmomaxillary ligament; no meniscus between premaxilla and maxilla. Unicuspid bi- or tri-serial outer teeth.

Dentary expanded medially, robust; coronoid process on dentary not overlapping with that of articular; retroarticular not elongate. Autopalatine with head angled anteriorly; ventral process elongate reaching quadrate; metapterygoid absent.

Orbital rim free; anterior naris not tubular; supraorbital sensory pores reduced; seven preopercular pores; four mandibular pores; three lacrimal pores.

Males larger than females; all fins rounded; body generally straw-colored overall; with faint midlateral reticulations.

No fatty predorsal ridge; swimbladder does not extend posteriorly beyond hemal spines.

DISTRIBUTION: As for the subfamily.

REMARKS: The genus and species was reviewed by Roberts (1970) who reiterated Myers's (1955) statement that it was most likely related to the procatopines, although its precise placement within a phylogeny of procatopines was not possible. Range of meristic characters is supplemented by data from Roberts (1970).

MATERIAL EXAMINED: Brazil: Rio Madeira at Borba: the paratypes as listed above; SU 50196 (3); Manaus: near Rio Negro: MCZ 46714 (11); Lago Hyanuary: MCZ 41367 (5); Manaus area: MCZ 49958 (4+/4); MCZ 46712 (21); MCZ 46713 (3*/64).

## SUPERFAMILY CYPRINODONTOIDEA

DIAGNOSIS: Distinguished from other cyprinodontiforms by the three derived characters: lateral ethmoid expanded medially and oriented so it lies perpendicular to the frontal; reduced autopterotic fossa; and inclinators of the anal fin greatly enlarged.

## FAMILY GOODEIDAE JORDAN

Type Genus *Goodea* Jordan, 1880.

DIAGNOSIS: Distingushed from other cyprinodontiform fishes by four derived characters: first two to seven middle anal radials fused to the proximal radials; dorsal processes of the maxillaries greatly reduced; distal arm of the maxilla straight, rather than curved; and articular greatly reduced.

COMPOSITION: Two subfamilies: Goodeinae Jordan and Empetrichthyinae Jordan, Evermann and Clark, as defined below.

DISTRIBUTION: Nevada; Death Valley system; Mesa Central, Mexico (fig. 82).

## SUBFAMILY EMPETRICHTHYINAE JORDAN, EVERMANN AND CLARK

Type Genus *Empetrichthys*, Gilbert, 1893.

DIAGNOSIS: Distinguished from other cyprinodontiforms by a derived first epibranchial and from other fishes of the Goodeidae by lacking pelvic fins and fin supports.

COMPOSITION: Two genera, *Empetrichthys* with two species, *merriami* Gilbert and *latos* Miller, the latter with three subspecies (*latos*, *pahrump* Miller, *concavus* Miller); *Crenichthys* with two species, *nevadae* Hubbs and *baileyi* (Gilbert).

DISTRIBUTION: Death Valley system and eastern Nevada.

## GENUS *EMPETRICHTHYS* GILBERT

*Empetrichthys* Gilbert, 1893, p. 233 (type species *Empetrichthys merriami* Gilbert, by original designation).

ETYMOLOGY: *Empetrichthys* from the Greek *em*, meaning within; *petros*, meaning rocks; and *ichthys*, meaning fish with rocks within, referring to the large molariform pharyngeal teeth.

TYPES: Nevada: Ash Meadows: *Empetrichthys merriami* Gilbert, Type, USNM 131151 (1).

COMPOSITION: As listed for the subfamily.

DIAGNOSIS: Distinguished from other members of the Goodeidae by having fleshy bases of the dorsal and anal fins, and greatly enlarged pharyngeal teeth.

DEFINITION: Anal: i, 13; Dorsal: i, 11; Pelvic: 0; Pectoral: 17; Caudal: 6, 18, 6; Vertebrae: 15+16; Gill rakers on the anterior arm of the first arch: 12–13. Branchiostegal rays: 6; Scales lateral series: 29–30.

First pleural rib on parapophysis of second vertebra; parapophysis not reduced; no pleural ribs on hemal spines; hypural plates fused into hypural fan. Epipleural ribs not bifid.

Anal fin not modified into a gonopodium; anal fin inclinators enlarged; first proximal radial present; first middle anal radial absent; second fused to second proximal radial.

Spermatozeugmata not formed; fertilization external; development nonannual; oviparous Eggs round.

One dorsal ray articulating with the first two dorsal radials; dorsal fin origin opposite origin of anal.

Autopterotic fossa reduced; lateral ethmoid expanded medially, reaching parasphenoid and lying perpendicular to frontal; parasphenoid not expanded anteriorly; no supraoccipital and exoccipital processes; neural arches of first vertebra open, not forming a spine; first vertebra articulates with skull via basioccipital and exoccipital condyles; supraoccipital excluded from formation of foramen magnum; parietals present; nasals expanded medially.

Mesethmoid ossified; pelvic fins and fin supports absent; interarcual cartilage reduced, attaches laterally to second pharyngobranchial with a bony flange; basihyal long and narrow; no tooth patches on second and third hypobranchials; teeth on fourth ceratobranchials; dorsal hypohyal absent; anterior extension of anterior ceratohyal ventral to ventral hypohyal; uncinate process on fourth epibranchial articulates with that of third; first epibranchial with indentation; interhyal ossified; two ossified basibranchials. Vomer with posterior extension ventral to parasphenoid.

Lacrimal flat and broad, carrying a distinct sensory canal; dermosphenotic and preopercular with a distinct sensory canal; pectoral girdle highset; first postcleithrum absent; posttemporal with ossified lower limb; posttemporal not fused to supracleithrum.

Vomer ossified, edentulous; medial arm of maxilla straight with reduced dorsal process; ventral arms not abutting rostral cartilage; outer arm narrow.

Premaxillary ascending processes narrow and reduced, not tapered posteriorly and not overlapping in the midline; rostral cartilage reduced; outer arm of premaxilla with alveolar process, indented posteriorly to form S-shaped arm. No ligament from the ventral arms of maxillaries to middle of rostral cartilage; no ethmomaxillary ligament; no meniscus between premaxilla and maxilla. Enlarged biserial outer teeth.

Dentary expanded medially, robust; coronoid process on dentary not overlapping with that of articular; articular reduced; retroarticular not elongate. Autopalatine with head angled anteriorly; ventral process elongate reaching quadrate; metapterygoid absent.

Orbital rim free; anterior naris not tubular; supraorbital sensory pores 1–2a, 2b–4, 5–7; seven preopercular pores; four mandibular pores; three lacrimal pores.

Females larger than males; fins rounded or truncate. Bases of anal and dorsal fins fleshy.

No fatty predorsal ridge; swimbladder does not extend posteriorly beyond hemal spines.

DISTRIBUTION: Death Valley, Nevada system.

REMARKS: The genus *Empetrichthys* was formerly assigned to the subfamily Fundulinae on the basis of primitive characters. Of the named taxa, all but one, *latos pahrump*, are extinct (Soltz and Naiman, 1978).

MATERIAL EXAMINED: *E. merriami*: Nevada: Ash Meadows: the type as listed above; Paratypes: USNM 46102 (2); Pahrump: SU 35966 (1*/15). *E. latos pahrump*: Nevada: Pahrump Ranch: CAS 22990 (1*/16).

FOSSILS: One species, *E. erdisi* Uyeno and Miller from the Pleistocene of Nevada, has been described (Uyeno and Miller, 1962).

### GENUS *CRENICHTHYS* HUBBS

*Crenichthys* Hubbs, 1932, p. 1 (type species *Crenichthys nevadae* Hubbs, by original designation).

ETYMOLOGY: *Crenichthys* from the Greek *cren*, meaning spring, and *ichthys* referring to the spring habitat of the genus.

TYPES: Nevada: Railroad Valley: *Crenichthys nevadae* Hubbs, Holotype MCZ 32948 (1).

COMPOSITION: As listed for the subfamily.

DIAGNOSIS: Distinguished from *Empetrichthys* by an outer row of bicupid teeth, and an increase in the number of gill rakers on the first arm to 20–22.

DEFINITION: Anal: i, 13; Dorsal: i, 11; Pelvic: 0; Pectoral: 16; Caudal: 9, 18, 9; Vertebrae: 11+17; Gill rakers on the anterior arm of the first arch: 20–22. Branchiostegal rays: 6; Scales lateral series: 26–28.

First pleural rib on parapophysis of second vertebra; parapophysis not reduced; no pleural ribs on hemal spines; hypural plates fused into hypural fan. Epipleural ribs not bifid.

Anal fin not modified into a gonopodium; anal fin inclinators enlarged; first proximal radial present; first five middle anal radials absent.

Spermatozeugmata not formed; fertilization external; development nonannual; oviparous. Eggs round.

One dorsal ray articulating with the first two dorsal radials; dorsal fin origin opposite origin of anal.

Autopterotic fossa reduced; lateral ethmoid expanded medially, reaching parasphenoid and lying perpendicular to frontal; parasphenoid not expanded anteriorly; no supraoccipital and exoccipital processes; neural arches of first vertebra open, not forming a spine; first vertebra articulates with skull via basioccipital and exoccipital condyles; supraoccipital excluded from formation of foramen magnum; parietals present; nasals expanded medially.

Mesethmoid ossified; pelvic fin and fin supports absent; interarcual cartilage reduced, attaches laterally to second pharyngobranchial with a bony flange; basihyal long and narrow; no tooth patches on second and third hypobranchials; teeth on fourth ceratobranchials; dorsal hypohyal absent; anterior extension of anterior ceratohyal ventral to ventral hypohyal; uncinate process on fourth epibranchial articulates with that of third; first epibranchial wide at its base; interhyal ossified; two ossified basibranchials. Vomer with posterior extension ventral to parasphenoid.

Lacrimal flat and broad, carrying a distinct sensory canal; dermosphenotic and preopercular with distinct sensory canal; pectoral girdle highset; first postcleithrum absent; posttemporal with ossified lower limb; posttemporal not fused to supracleithrum.

Vomer ossified, edentulous; medial arm of maxilla straight with reduced dorsal process; ventral arms not abutting rostral cartilage; outer arm narrow.

Premaxillary ascending processes narrow and reduced, not tapered posteriorly and not overlapping in the midline; rostral cartilage reduced or absent; outer arm of premaxilla with alveolar process, indented posteriorly to form S-shaped arm. No ligament from the ventral arms of maxillaries to middle of rostral cartilage; no ethmomaxillary ligament; no meniscus between premaxilla and maxilla. Bicuspid, biserial outer teeth.

Dentary expanded medially, robust; coronoid process on dentary not overlapping with that of articular; retroarticular not elongate. Autopalatine with head angled anteriorly; ventral process elongate reaching quadrate; metapterygoid absent.

Orbital rim free; anterior naris not tubular; supraorbital sensory pores 1–2a, 2b–4, 5–7; seven preopercular pores; four mandiublar pores; three lacrimal pores.

Femlaes larger than males; all fins rounded or truncate. Pigmentation pattern typically consisting of a series of midlateral dark blotches.

No fatty predorsal ridge; swimbladder does not extend posteriorly beyond hemal spines.

DISTRIBUTION: Nevada: Railroad Valley and White River Valley.

REMARKS: *Crenichthys*, as well as *Empetrichthys*, has been removed from a classification with the fundulines and placed in a monophyletic group with the goodeid fishes for the first time in this study.

MATERIAL EXAMINED: *C. nevadae*: the types as listed above: Nevada: Twin Springs Ranch: SU 48125 (2); *C. baileyi*: Nevada: Ash Springs: CAS 22980 (1*/42); USNM 11750 (2*/25); Aquarium material: AMNH 38408SW (4*/4).

## SUBFAMILY GOODEINAE JORDAN

DIAGNOSIS: Viviparous killifishes distinguished from cyprinodontiforms by shortened, unbranched anal fin rays in males crowded together and separated by a notch from the rest of the fin; first anal fin ray of males rudimentary; males with a pseudophallus; embryos with nutritive trophic processes; and ovaries united medially with ovigerous tissue partly to completely eliminated from the ovarian walls.

COMPOSITION: Approximately 36 species in 16 genera.

DISTRIBUTION: Mesa Central, Mexico with a concentration of species in the Rio Lerma Basin.

DEFINITION: Anal (i, ii) 11–13; Dorsal: i, 14–i, 15; Pelvic: 6; Pectoral: 15–16; Caudal: 8, 12, 8; Vertebrae: 16+21; Gill rakers on the anterior arm of the first arch: 27–29. Branchiostegal rays: 4–6; Scales lateral series: 30–35.

First pleural rib on parapophysis of second vertebra; parapophysis not reduced; no pleural ribs on hemal spines; hypural plates fused into hypural fan. Epipleural ribs not bifid.

Anal fin not modified into a gonopodium; anal fin inclinators enlarged; first proximal radial present; first five middle anal radials absent. First anal ray rudimentary in males.

Spermatozeugmata formed; fertilization internal; males possess a muscular organ responsible for the transfer of sperm; ovary fused with a concentration of ovigerous tissue in the outer regions; embryos withoutpocketings of the intestine termed trophotaeniae; fertilization in the ovary.

One dorsal ray articulating with the first two dorsal radials; dorsal fin origin opposite origin of anal.

Autopterotic fossa reduced; lateral ethmoid expanded medially, reaching parasphenoid and lying perpendicular to frontal; parasphenoid not expanded anteriorly; no supraoccipital and exoccipital processes; neural arches of first vertebra open, not forming a spine; first vertebra articulates with skull via basioccipital and exoccipital condyles; supraoccipital excluded from formation of foramen magnum; parietals present; nasals expanded medially.

Mesethmoid ossified; pelvic fin and fin supports absent; interarcual cartilage reduced, attaches laterally to second pharyngobranchial with a bony flange; basihyal long and narrow; no tooth patches on second and third hypobranchials; teeth on fourth ceratobranchials; dorsal hypohyal absent; anterior extension of anterior ceratohyal ventral to ventral hypohyal; uncinate process on fourth epibranchial articulates with that of third; first epibranchial wide at its base; interhyal ossified; two ossified basibranchials. Vomer with posterior extension ventral to parasphenoid.

Lacrimal flat and broad, carrying a distinct sensory canal; dermosphenotic and preopercular with distinct sensory canal; pectoral girdle highset; first postcleithrum absent; posttemporal with ossified lower limb; posttemporal not fused to supracleithrum.

Vomer ossified, edentulous; medial arm of maxilla straight with reduced dorsal process; ventral arms not abutting rostral cartilage; outer arm narrow.

Premaxillary ascending processes narrow and reduced, not tapered posteriorly and not overlapping in the midline; rostral cartilage reduced or absent; outer arm of premaxilla with alveolar process, indented posteriorly to form S-shaped arm; No ligament from the ventral arms of maxillaries to middle of rostral cartilage; no ethmomaxillary ligament; no meniscus between premaxilla and maxilla. Uni- or bi-cuspid outer teeth.

Dentary expanded medially, robust; coronoid process on dentary not overlapping with that of articular; retroarticular not elongate. Autopalatine with head angled anteriorly; ventral process elongate reaching quadrate; metapterygoid absent.

Orbital rim free; anterior naris not tubular; supraorbital sensory pores 1–2a, 2b–4a, 4b–7; seven preopercular pores; four mandibular pores; three lacrimal pores.

Females larger than males; all fins rounded or truncate.

No fatty predorsal ridge; swimbladder does not extend posteriorly beyond hemal spines.

REMARKS: It is stressed that the subfamily Goodeinae in this present study is equivalent to the family Goodeidae of former authors. Workers on the subfamily generally follow the classification of the group presented by Hubbs and Turner (1939) and suggestions for modifications of that classification by Miller and Fitzsimons (1971). In addition, several recommendations for a reclassification of the goodeids are made in this paper, including the suggestion that *Ataentiobius* is a derived member of the group and has secondarily lost trophotaeniae.

MATERIAL EXAMINED: *Ataeniobius toweri*: San Luis Potosi: SU 9396 (2); *Characodon lateralis*: Durango: CAS 40705 (2*/40); *Girardinichthys innominatus*: Lerma River Basin: SU 47063 (45); *Goodea luitpoldi*: AMNH 18622 (1+/7); *Ilyodon whitei*: Michoacan: CAS 16044 (2*/10); *Skiffia lermae*: Patzcuaro: SU 22342 (2*/20); *Xenendum xaliscone*: Jalisco: Paratypes, SU 6207 (4); *Xenotoca variata*: Jalisco: ex UMMZ 179760 (uncat at CAS) (15): *Zoogoneticus diazi*: Michoacan: USNM 218752 (2*/34).

FOSSILS: Goodeid fossils are known from Pleistocene and Miocene deposits, Mesa Central, Mexico (Alvarez and Arreola, 1972; Smith, Cavender and Miller 1975).

### FAMILY CYPRINODONTIDAE GILL

Type Genus *Cyprinodon* Lacépède, 1803.

DIAGNOSIS: Distinguished from other cyprinodontiforms by three derived characters: dorsal processes of the maxillaries expanded medially nearly meeting in the midline, and possessing a distinct groove; lateral arm of the maxilla greatly expanded; and, the toothplate of the fourth pharyngobranchial greatly reduced.

COMPOSITION: Two subfamilies, Cubanichthyinae, new subfamily, and Cyprinodontinae Gill, as described below.

DISTRIBUTION: North, South, and Middle America, the Caribbean; Mediterranean Anatolian regions, as detailed below.

### SUBFAMILY CUBANICHTHYINAE, NEW SUBFAMILY

Type Genus *Cubanichthys* Hubbs, 1924.

DIAGNOSIS: Distinguished from other cyprinodontiforms by four derived characters: an enlarged supraoccipital crest; an elongate dorsal process of the autopalatine; a supraorbital sensory pore pattern characterized by a large third pore; and from other primitive cyprinodontids in lacking an ossified lower limb of the posttemporal.

COMPOSITION: A single genus, *Cubanichthys* Hubbs, with two species: *cubensis* Eigenmann and *pengelleyi* (Fowler).

DISTRIBUTION: Cuba and Jamaica.

### GENUS *CUBANICHTHYS* HUBBS

*Cubanichthys* Hubbs, 1926, p. 4 (type species *Fundulus cubensis* Eigenmann, by original designation).

*Chriopeoides* Fowler, 1939, p. 4 (type species *Chriopeoides pengelleyi* Fowler, by original designation).

ETYMOLOGY: *Cubanichthys*, after Cuba to which the species *cubensis* is endemic.

TYPES: Cuba: Pinar del Rio: *Fundulus cubensis* Eigenmann; IU 9887 (3).

COMPOSITION: As for the subfamily.

DIAGNOSIS: As for the subfamily.

DEFINITION: Anal: i, 9; Dorsal: ii, 9; Pelvic: 6; Pectoral: 18; Caudal: 7, 10, 7; Vertebrae: 11+16; Gill rakers on the anterior arm of the first arch: 9. Branchiostegal rays: 6; Scales lateral series: 24–26.

First pleural rib on parapophysis of second vertebra; parapophysis not reduced; no pleural ribs on hemal spines; hypural plates fused into hypural fan. Epipleural ribs not bifid.

Anal fin not modified into a gonopodium; anal fin inclinators enlarged; first proximal radial present; middle anal radials present.

Spermatozeugmata not formed; fertilization external; development nonannual; oviparous. Eggs round.

One dorsal ray articulating with the first two dorsal radials; dorsal fin origin opposite origin of anal.

Autopterotic fossa reduced; lateral ethmoid expanded medially, reaching parasphenoid and lying perpendicular to frontal; parasphenoid not expanded anteriorly; supraoccipital crest present; neural arches of first vertebra open, not forming a spine; first vertebra articulates with skull via basioccipital and exoccipital condyles; supraoccipital excluded from formation of foramen magnum; parietals present; nasals expanded medially.

Mesethmoid ossified; medial processes of pelvic fin base and ischial process not reduced; interarcual cartilage reduced, attaches laterally to second pharyngobranchial with a bony flange; basihyal long and narrow; no tooth patches on second and third hypobranchials; teeth on fourth ceratobranchials; dorsal hypohyal absent; anterior extension of anterior ceratohyal ventral to ventral hypohyal; uncinate process on fourth epibranchial articulates with that of third; first epibranchial wide at its base; interhyal ossified; two ossified basibranchials. Vomer with posterior extension ventral to parasphenoid.

Lacrimal flat and broad, carrying a distinct sensory canal; dermosphenotic and preopercular with distinct sensory canal; pectoral girdle lowset; first postcleithrum present; posttemporal with unossified lower limb; posttemporal not fused to supracleithrum.

Vomer ossified, edentulous; medial arm of maxilla straight with pronounced dorsal processes with a groove, nearly meeting in the midline; ventral arms narrow, not abutting rostral cartilage; outer arm robust.

Premaxillary ascending processes narrow and reduced, not tapered posteriorly and not overlapping in the midline; rostral cartilage reduced; outer arm of premaxilla with alveolar process, indented posteriorly to form S-shaped arm; No ligament from the ventral arms of maxillaries to middle of rostral cartilage; no ethmomaxillary ligament; no meniscus between premaxilla and maxilla. Unicuspid bi- or tri-serial outer teeth.

Dentary expanded medially, robust; coronoid process on dentary not overlapping with that of articular; retroarticular not elongate. Autopalatine with head angled anteriorly, elongate dorsal process; ventral process elongate reaching quadrate; metapterygoid absent.

Orbital rim free; anterior naris not tubular; supraorbital sensory pores 1–2a, an enlarged 3, 4b–7; seven preopercular pores; four mandibular pores; three lacrimal pores.

Females larger than males; males with dorsal fin enlarged; caudal truncate; pigmentation pattern consisting of a dark lateral band extending from the eye onto the caudal peduncle.

No fatty predorsal ridge; swimbladder does not extend posteriorly beyond hemal spines.

DISTRIBUTION: As for the subfamily.

REMARKS: Both *cubensis* and *pengelleyi* were classified in the subfamily Fundulinae prior to this study. The generic name *Chriopeoides* refers to the resemblance of *pengelleyi* to the North American *Lucania* (*Chriopeops*) *goodei*. Also, *cubensis* had been considered an island form of the wholly North American *Lucania* (Hubbs and Miller, 1965; Rosen, 1976). Foster (1969) provided observations on the habitat and locality of *pengelleyi*.

MATERIAL EXAMINED: Cuba: Pinar del Rio, Syntypes as listed above, *C. cubensis* ANSP 60283–87 (1*/4); Jamaica: St. Elizabeth's Parish; Black River Drainage: *C. pengelleyi* ANSP 112908 (1*/64).

### SUBFAMILY CYPRINODONTINAE GILL

DIAGNOSIS: Distinguished from all other cyprinodontiforms by three uniquely derived characters: second pharyngobranchial offset to the third; Meckel's cartilage expanded posteriorly; and, transverse processes of the vertebrae reduced and cup-shaped; and by two independently derived characters: parietals absent, and uniserial outer jaw teeth.

COMPOSITION: Two tribes, Cyprinodontini Gill and Orestiini Bleeker, as described below.

DISTRIBUTION: As for the tribes listed below.

### TRIBE ORESTIINI BLEEKER

DIAGNOSIS: Distinguished from all other cyprinodontiform fishes by an extremely robust lower jaw caused by a medial extension of the dentary.

COMPOSITION: Four genera and approximately 65 species: *Aphanius* Nardo, "*Aphanius*," *Kosswigichthys* Sozer, and *Orestias* Valenciennes.

DISTRIBUTION: (fig. 86) Mediterranean region: North Africa, Spain, Italy, Turkey, Greece, and Mediterranean islands, as well as the Saudi Arabian Peninsula and Iran.

### GENUS *APHANIUS* NARDO

*Aphanius* Nardo, 1827, p. 48 (type species *Aphanius fasciatus* Nardo, by subsequent designation).

*Lebias* Cuvier, 1817, p. 119 (type species *Aphanius fasciatus* Nardo, by monotypy).

*Tellia* Gervais, 1853, p. 15 (type species *Tellia apoda* Gervais, by original designation).

*Micromugil* Gulia, 1861, p. 11 (type species *Aphanius faciatus* Nardo, by monotypy).

*Aphaniops* Hoedeman, 1951, p. 2 (type species *Lebias dispar* Ruppell, by original designation).

ETYMOLOGY: *Aphanius* from the Greek *aphanes*, meaning secret or unknown in reference to the cyprinodonts of the Anatolian region.

COMPOSITION: Approximately 30 species, as listed in Lazara (1979), minus those of the *mento*-complex that are referred to the genus "*Aphanius*."

DIAGNOSIS: Distinguished from other members of the tribe Orestiini by three primitive characters: cephalic sensory pore pattern represented by pores rather than reduced to neuromasts; a urohyal that is not embedded in the urohyal membranes; and an ossified interhyal.

DEFINITION: Anal: ii, 8; Dorsal: i, 9; Pelvic: 6; Pectoral: 15–16; Caudal: 7, 14, 7; Vertebrae: 11+15; Gill rakers on the anterior arm of the first arch: 8–10. Branchiostegal rays: 5; Scales lateral series: 23–26.

First pleural rib on parapophysis of second vertebra; parapophysis reduced; no pleural ribs on hemal spines; hypural plates fused into hypural fan. Epipleural ribs not bifid.

Anal fin not modified into a gonopodium; anal fin inclinators enlarged; first proximal radial present; middle anal radials present.

Spermatozeugmata not formed; fertilization external; development nonannual; oviparous. Eggs round.

One dorsal ray articulating with the first two dorsal radials; dorsal fin origin opposite origin of anal.

Autopterotic fossa reduced; lateral ethmoid expanded medially, reaching parasphenoid and lying perpendicular to frontal; parasphenoid not expanded anteriorly; no supraoccipital and exoccipital processes; neural arches of first vertebra open, not forming a spine; first vertebra articulates with skull via basioccipital and exoccipital condyles, exoccipital condyles reduced; supraoccipital excluded from formation of foramen magnum; parietals absent; nasals expanded medially.

Mesethmoid unossified; medial processes of pelvic fin base and ischial process not reduced; interarcual cartilage reduced, attaches laterally to second pharygobranchial with a flange and oriented dorsally; basihyal long and narrow; no tooth patches on second and third hypobranchials; teeth on fourth ceratobranchials; dorsal hypohyal absent; anterior extension of anterior ceratohyal ventral to ventral hypohyal; uncinate process on fourth epibranchial articulates with that of third; first epibranchial wide at its base; interhyal ossified; two ossified basibranchials. Vomer with posterior extension ventral to parasphenoid.

Lacrimal flat and broad, carrying a distinct sensory canal; dermosphenotic and preopercular with distinct sensory canal; pectoral girdle lowset; first postcleithrum present; posttemporal with ossified lower limb; posttemporal not fused to supracleithrum.

Vomer ossified, edentulous; medial arm of maxilla straight with pronounced dorsal processes with a groove, nearly meeting in the midline; ventral arms narrow, not abutting rostral cartilage; outer arm robust.

Premaxillary ascending processes narrow and reduced, not tapered posteriorly and not overlapping in the midline; rostral cartilage reduced; outer arm of premaxilla with alveolar process, indented posteriorly to form S-shaped arm. No ligament from the ventral arms of maxillaries to middle of rostral cartilage; no ethmomaxillary ligament; no meniscus between premaxilla and maxilla. Tricuspid, uniserial outer teeth.

Dentary with medial extension, robust; coronoid process on dentary not overlapping with that of articular; retroarticular not elongate. Autopalatine with head angled anteriorly; ventral process elongate reaching quadrate; metapterygoid absent.

Orbital rim free; anterior naris not tubular; supraorbital sensory pores 1–4a, 4b–7; seven preopercular pores; four mandibular pores; three lacrimal pores.

Females larger than males; males often with enlarged dorsal and anal fins; caudal fin rounded or truncate.

No fatty predorsal ridge; swimbladder does not extend posteriorly beyond hemal spines.

DISTRIBUTION: Mediterranean, along the north coast of Africa, Spain, Italy, along the periphery of the Saudi Arabian Peninsula; Turkey and Greece.

REMARKS: The genus *Aphanius* as the term is used here references those species of the genus assessed as the most plesiomorphic of the Anatolian cyprinodonts and *Orestias*. The more apomorphic species are placed in "*Aphanius*."

MATERIAL EXAMINED: *A. fasciatus*: Aquarium material: AMNH 36770SW (3*/7); BMNH 1958.3.3:551–580 (30); *A. dispar*: Abyssinia: Syntype: BMNH 1860.11.9:152 (1/3); Saudi Arabia: Persian Gulf: USNM 147834 (41); BMNH 1977.12.13:1–490. (2*/490); *A. apoda*: Algeria: BMNH 1958.4.22: 1–7 (7).

FOSSILS: Fossil cyprinodontiforms of the Old World primarily in the Mediterranean region have been assigned to the genus *Aphanius* or to new fossil taxa:

### GENUS *PROLEBIAS* SAUVAGE

*Prolebias* Sauvage, 1874, p. 187 (type species *Lebias cephalotes* Agassiz, by original designation). (Oligocene and Miocene of Western Europe.)

### GENUS *PACHYLEBIAS* WOODWARD

*Pachylebias* Woodward, 1901, p. 294 (type species *Lebias crassicaudus* Agassiz, by original designation ). (Miocene of Italy and Crete.)

### GENUS *BRACHYLEBIAS* PRIEM

*Brachylebias* Priem, 1908, p. 21 (type species *Brachylebias persicus* Priem, by original designation). (Miocene of Iran.)

### GENUS "*APHANIUS*"

ETYMOLOGY: The genus "*Aphanius*" is used as a reference for the *Aphanius mento*-complex hypothesized to be more closely related to *Kosswigichthys* and *Orestias* than to other *Aphanius*.

COMPOSITION: Species of the *Aphanius mento*-complex including *mento* (Heckel) and *chantrei* (Gaillard).

DIAGNOSIS: Distinguished from other *Aphanius* species by a urohyal embedded in the fold of the branchiostegal membranes and a derived head pore pattern.

DEFINITION: Anal: i, 11; Dorsal: i, 9; Pelvic: 6; Pectoral: 15–16; Caudal: 7, 14, 7; Vertebrae: 12+14; Gill rakers on the anterior arm of the first arch: 8–10. Branchiostegal rays: 5; Scales lateral series: 23–26.

First pleural rib on parapophysis of second vertebra; parapophysis reduced; no pleural ribs on hemal spines; hypural plates fused into hypural fan. Epipleural ribs not bifid.

Anal fin not modified into a gonopodium; anal fin inclinators enlarged; first proximal radial present; middle anal radials present.

Spermatozeugmata not formed; fertilization external; development nonannual; oviparous. Eggs round.

One dorsal ray articulating with the first two dorsal radials; dorsal fin origin opposite origin of anal.

Autopterotic fossa reduced; lateral ethmoid expanded medially, reaching parasphenoid and lying perpendicular to frontal; parasphenoid not expanded anteriorly; no supraoccipital and exoccipital processes; neural arches of first vertebra open, not forming a spine; first vertebra articulates with skull via basioccipital and exoccipital condyles; supraoccipital excluded from formation of foramen magnum; parietals absent; nasals expanded medially.

Mesethmoid unossified; medial processes of pelvic fin base and ischial process not reduced; interarcual cartilage reduced, attaches laterally to second pharyngobranchial with a bony flange and oriented dorsally; basihyal long and narrow; no tooth patches on second and third hypobranchials; teeth on fourth ceratobranchials; dorsal hypohyal absent; anterior extension of anterior ceratohyal ventral to ventral hypohyal; uncinate process on fourth epibranchial articulates with that of third; first epibranchial wide at its base; interhyal ossified; two ossified basibranchials. Vomer with posterior extension ventral to parasphenoid.

Lacrimal flat and broad, carrying a distinct sensory canal; dermosphenotic and preopercular with distinct sensory canal; pectoral girdle lowset; first postcleithrum present; posttemporal with ossified lower limb; posttemporal not fused to supracleithrum.

Vomer ossified, edentulous; medial arm of maxilla straight with pronounced dorsal processes with a groove, nearly meeting in the midline; ventral arms narrow, not abutting rostral cartilage; outer arm robust.

Premaxillary ascending processes narrow and reduced, not tapered posteriorly and not overlapping in the midline; rostral cartilage reduced; outer arm of premaxilla with alveolar process, indented posteriorly to form S-shaped arm. No ligament from the ventral arms of maxillaries to middle of rostral cartilage; not ethmomaxillary ligament; no meniscus between premaxilla and maxilla. Tricuspid, uniserial outer teeth.

Dentary with medial extension, robust; coronoid process on dentary not overlapping with that of articular; retroarticular not elongate. Autopalatine with head angled anteriorly; ventral process elongate reaching quadrate; metapterygoid absent, urohyal embedded in branchiostegal membranes.

Orbital rim free; anterior naris not tubular; cephalic sensory pores reduced to a series of neuromasts.

Females larger than males; males often with enlarged dorsal and anal fins; caudal fin rounded or truncate.

No fatty predorsal ridge; swimbladder does not extend posteriorly beyond hemal spines.

DISTRIBUTION: The Mediterranean (Spain, Italy) and western Turkey.

REMARKS: The genus "*Aphanius*" is used as a reference for derived species of *Aphanius*. It is not formally named as a new genus since its limits cannot readily be defined and may be expanded to include more species still referenced in the genus *Aphanius*.

MATERIAL EXAMINED: *A. mento*: Aquarium material: AMNH 28610 (2+/1*/9).

### GENUS *KOSSWIGICHTHYS* SOZER

*Kosswigichthys* Sozer, 1942, p. 308 (type species *Kosswigichthys asquamatus* Sozer, by original designation).

*Anatolichthys* Kosswig and Sozer, 1945, p. 77 (type species *Anatolichthys splendens* Kosswig and Sozer, by original designation).

ETYMOLOGY: *Kosswigichthys*, in honor of Curt Kosswig, prominent ichthyologist of fishes of the Anatolian region.

COMPOSITION: Four species: *asquamatus* Sozer, *burdurensis* (Askiray), *splendens* (Kosswig and Sozer), *transgrediens* (Askiray).

DIAGNOSIS: Distinguished from other members of the tribe Orestiini by lacking the dermosphenotic.

DEFINITION: Anal: i, 10; Dorsal: i, 9; Pelvic: 6–7; Pectoral: 12; Caudal: 8, 10, 8; Vertebrae: 11+17–12+17; Gill rakers on the anterior arm of the first arch: 10–12. Branchiostegal rays: 5; Scales lateral series: 0–30.

First pleural rib on parapophysis of second vertebra; parapophysis reduced; no pleural ribs on hemal spines; hypural plates fused into hypural fan. Epipleural ribs not bifid.

Anal fin not modified into a gonopodium; anal fin inclinators enlarged; first proximal radial present; middle anal radials present.

Spermatozeugmata not formed; fertilization external; development nonannual; oviparous. Eggs round.

One dorsal ray articulating with the first two dorsal radials; dorsal fin origin opposite origin of anal.

Autopterotic fossa reduced; lateral ethmoid expanded medially, reaching parasphenoid and lying perpendicular to frontal; parasphenoid not expanded anteriorly; no supraoccipital and exoccipital processes; neural arches of first vertebra open, not forming a spine; first vertebra articulates with skull via basioccipital and exoccipital condyles, exoccipital condyles reduced; supraoccipital excluded from formation of foramen magnum; parietals absent; nasals expanded medially.

Mesethmoid unossified; medial processes of pelvic fin base and ischial process not reduced; interarcual cartilage reduced, attaches laterally to second pharyngobranchial with a bony flange and oriented dorsally; basihyal long and narrow; no tooth patches on second and third hypobranchials; teeth on fourth ceratobranchials; dorsal hypohyal absent; anterior extension of anterior ceratohyal ventral to ventral hypohyal; uncinate process on fourth epibranchial articulates with that of third; first epibranchial wide at its base; interhyal unossified; two ossified basibranchials. Vomer with posterior extension ventral to parasphenoid.

Lacrimal flat and broad, carrying a distinct sensory canal; dermosphenotic absent; preopercular with distinct sensory canal; pectoral girdle lowset; first postcleithrum present; posttemporal with unossified lower limb; posttemporal not fused to supracleithrum.

Vomer ossified, edentulous; medial arm of maxilla straight with pronounced dorsal processes with a groove, nearly meeting in the midline; ventral arms narrow, not abutting rostral cartilage; outer arm robust.

Premaxillary ascending processes narrow and reduced, not tapered posteriorly and not overlapping in the midline; rostral cartilage reduced or absent; outer arm of premaxilla with alveolar process, indented posteriorly to form S-shaped arm. No ligament from the ventral arms of maxillaries to middle of rostral cartilage; no ethmomaxillary ligament; no meniscus between premaxilla and maxilla. Uni- or tri-cuspid uniserial outer teeth.

Dentary with medial extension, robust; coronoid process on dentary not overlapping with that of articular; retroarticular not elongate. Autopalatine with head angled anteriorly; ventral process elongate reaching quadrate; metapterygoid absent.

Orbital rim free; anterior naris not tubular; cephalic sensory pores reduced to derived neuromast pattern or absent.

Females larger than males; males never with fin extensions; caudal fin truncate; scales reduced or absent.

No fatty predorsal ridge; swimbladder does not extend posteriorly beyond hemal spines.

DISTRIBUTION: Freshwater lakes of Turkey.

REMARKS: *Kosswigichthys* has been synonymized with *Aphanius* by many authors; it is hypothesized, however, that the genus is more closely related to *Orestias* than to other Anatolian cyprinodontines. This association produces one of the more unusual distributional patterns within the group.

MATERIAL EXAMINED: *K. asquamatus*: Aquarium material: AMNH 28622 (2+/5); Turkey: ANSP 89883 (1*/6); BMNH 1948.3.15:40–43 (1*/3); *K. transgrediens*: Acy Gol- Akpinar ANSP 89890 (6); *K. splendens*: Turkey: SU 15830 (2*/15).

### GENUS *ORESTIAS* VALENCIENNES

*Orestias* Valenciennes, 1839, p. 118 (type species *Orestias cuvieri* Valenciennes, by subsequent designation).

*Protorestias* Allen (in Eigenmann and Allen), 1942, p. 353 (hypothetical ancestral genus of *Orestias*, no type designated).

ETYMOLOGY: *Orestias*, after the Greek mythological figure Orestes, said to have been hidden in the mountains, in reference to the unique distribution of the genus in the high-altitude lakes of the Andes.

TYPES: Peru: Lake Titicaca: *Orestias cuvieri* Valenciennes, MHNH.

DIAGNOSIS: Distinguished from other members of the family Cyprinodontidae by an absence of pelvic fins and fin supports, absence of a vomer, and absence of a first postcleithrum.

DEFINITION: Anal: i, 13: Dorsal: i, 13; Pelvic: 0; Pectoral: 15–17; Caudal: 8, 15, 8; Vertebrae: 15+16–15+18; Gill rakers on the anterior arm of the first arch: 9–24. Branchiostegal rays: 5–6; Scales lateral series: 0–54.

First pleural rib on parapophysis of second vertebra; parapophysis not reduced; no pleural ribs on hemal spines; hypural plates fused into hypural fan. Epipleural ribs bifid or not.

Anal fin not modified into a gonopodium; anal fin inclinators enlarged; first proximal radial present; middle anal radials present.

Spermatozeugmata not formed; fertilization external; development nonannual; oviparous. Eggs round.

One dorsal ray articulating with the first two dorsal radials; dorsal fin origin opposite origin of anal.

Autopterotic fossa reduced; lateral ethmoid expanded medially, reaching parasphenoid and lying perpendicular to frontal; parasphenoid not expanded anteriorly; no supraoccipital and exoccipital processes; neural arches of first vertebra open, not forming a spine; first vertebra articulates with skull via basioccipital and exoccipital condyles, exoccipital condyles reduced; supraoccipital excluded from formation of foramen magnum; parietals absent; nasals expanded medially.

Mesethmoid ossified; pelvic fin and fin supports absent; interarcual cartilage reduced, attaches laterally to second pharyngobranchial with a bony flange; basihyal long and narrow; no tooth patches on second and third hypobranchials; teeth on fourth ceratobranchials; dorsal hypohyal absent; no anterior extension of anterior ceratohyal ventral to ventral hypohyal; uncinate process on fourth epibranchial articulates with that of third; first epibranchial wide at its base; interhyal not ossified; two ossified basibranchials. Vomer with posterior extension ventral to parasphenoid.

Lacrimal flat and braod, carrying a distinct sensory canal; dermosphenotic reduced; preopercular with reduced sensory canal; pectoral girdle lowset; first postcleithrum absent; posttemporal with unossified lower limb; posttemporal not fused to supracleithrum.

Vomer absent; medial arm of maxilla straight with pronounced dorsal processes with a groove, nearly meeting in the midline; ventral arms narrow, not abutting rostral cartilage; outer arm robust.

Premaxillary ascending processes narrow and reduced, not tapered posteriorly and not overlapping in the midline; rostral cartilage reduced or absent; outer arm of premaxilla with alveolar process, indented posteriorly to form S-shaped arm. No ligament from the ventral arms of maxillaries to middle of rostral cartilage; no ethmomaxillary ligament;

no meniscus between premaxilla and maxilla. Uni- or bi-cuspid uniserial outer teeth.

Dentary with medial extension, robust; coronoid process on dentary not overlapping with that of articular; retroarticular not elongate. Autopalatine with head angled anteriorly; ventral process elongate reaching quadrate; metapterygoid absent.

Orbital rim free; anterior naris not tubular; cephalic sensory pore system represented by derived, lyre-shaped pattern of minute neuromasts.

Females larger than males; all fins rounded; scales present or absent.

No fatty predorsal ridge; swimbladder does not extend posteriorly beyond hemal spines.

DISTRIBUTION: (fig. 85) High-altitude lakes of the South American continental divide. Known range from Lago Ascotan, Chile north to Lago Llascha, Peru.

REMARKS: The distribution above represents a range extension of the genus. Specimens were collected by Tim Hardin of Colorado State University on June 13, 1979. The placement of the genus *Orestias* in the tribe Orestiini along with the Anatolian cyprinodontines represents the first statement concerning its relationship to other cyprinodontiforms since the tentative statements by Eigenmann (1920) and Foster (1967).

MATERIAL EXAMINED: *O. cuvieri*: Lake Titicaca: SU 9331 (1); BMNH 1944.6.6.:1–6 (6); *O. pentlandi*: Lake Titicaca: Puno Bay: AMNH 1117 (1), BMNH 1944.6.6.:22–25 (3); *O. agassi*: Peru: Rio Caminaque, near Lake Titicaca: CAS 42534 (20); *O. mooni*: Lake Titicaca: Puno Bay: Syntype, USNM 133139 (1); *O. polonorum*: Peru: Lake Junin: Type, BMNH 1944.6.6.:223 (1); species unidentified: Peru: Challhuacocha: CAS 40700 (2*/42); Bolivia: tributary of Lake Titicaca: AMNH 20355SW (2*/60); AMNH 20353SW (2+/8); Peru: Lago Llascha: AMNH 38411(3).

## TRIBE *CYPRINODONTINI* GILL

DIAGNOSIS: Distinguished from all other cyprinodontiforms by the following derived characters: a derived form of the attachment of the first vertebra to the skull with supraoccipital forming, rather than excluded from, the dorsal wall of the foramen magnum, and neurapophyses of the first vertebra angled forward and firmly applied to the skull, and no exoccipital condyles; and pharyngobranchial teeth in discrete rows.

COMPOSITION: Five genera and approximately 40 species: *Cyprinodon* Lacépède, *Megupsilon* Miller and Walters, *Jordanella* Goode and Bean, *Cualac* Miller and *Floridichthys* Hubbs.

DISTRIBUTION: North and Middle America to Honduras; the West Indies southward to Venezuela (fig. 88).

FOSSILS: In addition to the species referred to the genus *Cyprinodon* (Miller, 1945) of California, a fossil genus, *Carrionellus* (White, 1927) from the Lower Miocene of Ecuador has been referred to the cyprinodontines on the basis of its overall fin position and the possession of tricuspid teeth in the jaws. The outer teeth, however, are in two rows, not one as in the cyprinodontines. I suggest that *Carrionellus* is perhaps a characoid rather than a cyprinodont since in that group biserial tricuspid teeth are not uncommon, and the condition is unknown in the cyprinodontines.

## GENUS *CYPRINODON* LACÉPÈDE

*Cyprinodon* Lacépède, 1803, p. 486 (type species *Cyprinodon variegatus* Lacépède by original designation).

*Prinodon* Rafinesque, 1815, p. 88 (type species *Cyprinodon variegatus* Lacépède, by original designation [proposed as a substitute for *Cyprinodon* which was considered to be too long a name]).

*Encrotes* Gistel, 1848, p. 9 (type species *Cyprinodon variegatus* Lacépède, by original designation [proposed as a substitute for *Lebia* or *Lebias* Cuvier]).

*Trifarcius* Poey, 1860, p. 306 (type species *Trifarcius riverendi* Poey, by original designation).

ETYMOLOGY: *Cyprinodon* from *Cyprinus* and *odon*, meaning teeth, referring to the genus as a minnow with teeth.

COMPOSITION: Approximately 36 species as listed in Lazara (1979).

DIAGNOSIS: Cyprinodontines with an enlarged scapular process.

DEFINITIONS: Anal: (i), 9–10; Dorsal: ii, 9; Pelvic: 0–7; Pectoral: 14–16; Caudal: 7, 12, 7;. Vertebrae: 12+12–12+14. Gill rakers on the anterior arm of the first arch: 14–23. Branchiostegal rays: 5; Scales lateral series: 24–28.

First pleural rib on parapophysis of second vertebra; parapophysis not reduced; no pleural ribs on hemal spines; hypural plates fused into hypural fan; Epipleural ribs not bifid.

Anal fin not modified into a gonopodium; anal fin musculature unmodified; first proximal radial present; middle anal radials present.

Spermatozeugmata not formed; fertilization external; development nonannual; oviparous. Eggs round.

One dorsal ray articulating with the first two dorsal radials; dorsal fin origin opposite origin of anal.

Autopterotic fossa reduced; lateral ethmoid expanded medially, reaching parasphenoid and lying perpendicular to frontal; parasphenoid not expanded anteriorly; no supraoccipital and exoccipital processes; neural arches of first vertebra open and applied to skull; first vertebra articulates with skull via basioccipital condyles; exoccipital condyles absent; supraoccipital included in formation of foramen magnum; parietals absent; nasals expanded medially.

Mesethmoid ossified; medial processes of pelvic fin base and ischial process not reduced, or pelvics absent; interarcual cartilage reduced, attaches laterally to second pharyngobranchial with a bony flange; pharyngobranchial teeth arranged in discrete rows; basihyal long and narrow; no tooth patches on second and third hypobranchials; teeth on fourth ceratobranchials; dorsal hypohyal absent; anterior extension of anterior ceratohyal ventral to ventral hypohyal; uncinate process on fourth epibranchial articulates with that of third; first epibranchial wide at its base; interhyal ossified; two ossified basibranchials. Vomer with posterior extension ventral to parasphenoid.

Lacrimal flat and broad, carrying a distinct sensory canal; dermosphenotic and preopercular with distinct sensory canal; pectoral girdle low-set; first postcleithrum present; scapular process enlarged; posttemporal with ossified lower limb; posttemporal not fused to supracleithrum.

Vomer ossified, edentulous; medial arm of maxilla straight with pronounced dorsal processes with a groove, nearly meeting in the midline; ventral arms narrow, not abutting rostral cartilage; outer arm robust.

Premaxillary ascending processes narrow and reduced, not tapered posteriorly and not overlapping in the midline; rostral cartilage reduced or absent; outer arm of premaxilla with alveolar process, indented posteriorly to form S-shaped arm; No ligament from the ventral arms of maxillaries to middle of rostral cartilage; no ethmomaxillary ligament; no meniscus between premaxilla and maxilla. Tricuspid, uniserial outer teeth.

Dentary expanded medially, robust; coronoid process on dentary not overlapping with that of articular; retroarticular not elongate. Autopalatine with head angled anteriorly; ventral process elongate reaching quadrate; metapterygoid absent.

Orbital rim free; anterior naris not tubular; supraorbital sensory pores 1–7; seven preopercular pores; two mandibular pores; three lacrimal pores.

Females and males of equal sizes or males larger; males without fin extensions; males often with a dark caudal margin; usually a spot at the base of dorsal fin.

No fatty predorsal ridge; swimbladder does not extend posteriorly beyond hemal spines.

DISTRIBUTION: North and Middle America, the West Indies to Venezuela.

REMARKS: Since all species have not been examined, *Cyprinodon* is only tentatively identified as monophyletic by a greatly enlarged scapular process.

MATERIAL EXAMINED: *C. variegatus*: New York: Long Island: AMNH 36072 (4*/97); AMNH 21800 (1+); Alabama: AMNH 35750 (4). *C. diabolis*: Nevada: Devil's Hole: CAS 22994 (16); *C. bondi*: Haiti: Etang Saumatre AMNH 377341 (12); *C. macularius*: Nevada: Nye Co., AMNH 20232 (17).

### GENUS *JORDANELLA* GOODE AND BEAN

*Jordanella* Goode and Bean, 1879, p. 117 (type species *Jordanella floridae* Goode and Bean, by original designation).

*Garmanella* Hubbs, 1936, p. 218 (type species *Garmanella pulchra* Hubbs, by original designation).

ETYMOLOGY: *Jordanella* in honor of the American ichthyologist David Starr Jordan.

TYPES: Florida: *Jordanella floridae* Goode and Bean, Types, USNM 22903 (3).

COMPOSITION: Two species *floridae* Goode and Bean, and *pulchra* (Hubbs).

DIAGNOSIS: Distinguished from other cyprinodontoids by an elongate dorsal fin of 15 or more rays, and a dark suborbital bar.

DEFINITION: Anal: i, 10; Dorsal: (i or I) 14–17; Pelvic: 6–7; Pectoral: 15–16; Caudal: 6, 18, 6; Vertebrae: 12+14; Gill rakers on the anterior arm of the first arch: 10–12. Branchiostegal rays: 5; Scales lateral series: 24–26.

First pleural rib on parapophysis of second vertebra; parapophysis not reduced; no pleural ribs on hemal spines; hypural plates fused into hypural fan. Epipleural ribs not bifid.

Anal fin not modified into a gonopodium; anal fin musculature unmodified; first proximal radial present; middle anal radials present.

Spermatozeugmata not formed; fertilization external; development nonannual; oviparous. Eggs round.

One dorsal ray articulating with the first two dorsal radials; dorsal fin origin opposite origin of anal.

Autopterotic fossa reduced; lateral ethmoid expanded medially, reaching parasphenoid and lying perpendicular to frontal; parasphenoid not expanded anteriorly; no supraoccipital and exoccipital processs; neural arches of first vertebra open and applied to skull; first vertebra articulates with skull via basioccipital condyles; exoccipital condyles absent; supraoccipital included in formation of foramen magnum; parietals absent; nasals expanded medially.

Mesethmoid ossified; medial processes of pelvic fin base and ischial process not reduced; interarcual cartilage reduced, attaches laterally to second pharyngobranchial toothplate with a bony flange; pharyngobranchial teeth arranged in discrete rows; basihyal long and narrow; no tooth patches on second and third hypobranchials; teeth on fourth ceratobranchials; dorsal hypohyal absent; anterior extension of anterior ceratohyal ventral to ventral hypohyal; uncinate process on fourth epibranchial articulates with that of third; first epibranchial wide at its base; interhyal ossified; two ossified basibranchials. Vomer with posterior extension ventral to parasphenoid.

Lacrimal flat and broad, carrying a distinct sensory canal; dermosphenotic and preopercular with distinct sensory canal; pectoral girdle lowset; first postcleithrum present; posttemporal with ossified lower limb; posttemporal not fused to supracleithrum.

Vomer ossified, edentulous; medial arm of maxilla straight with pronounced dorsal processes with a groove, nearly meeting in the midline; ventral arms narrow, not abutting rostral cartilage; outer arm robust.

Premaxillary ascending processes narrow and reduced, not tapered posteriorly and not overlapping in the midline; rostral cartilage reduced or absent; outer arm of premaxilla with alveolar process, indented posteriorly to form S-shaped arm. No ligament from the ventral arms of maxillaries to middle of rostral cartilage; no ethmomaxillary ligament; no meniscus between premaxilla and maxilla. Tricuspid, uniserial outer teeth.

Dentary expanded medially, robust; coronoid process on dentary not overlapping with that of articular; retroarticular not elongate. Autopalatine with head angled anteriorly; ventral process elongate reaching quadrate; metapterygoid absent.

Orbital rim free; anterior naris not tubular; supraorbital sensory pores 1–7 or 1–3, 4–7; seven preopercular pores; no mandibular pores; three lacrimal pores.

Females and males of equal sizes or males larger; all fins rounded. Pigmentation pattern consisting of a prominent midlateral blotch, and a suborbital bar.

No fatty predorsal ridge; swimbladder does not extend posteriorly beyond hemal spines.

DISTRIBUTION: Florida and the Yucatan peninsula, south to Belize.

REMARKS: All workers on the cyprinodontines have remarked on the derived similarity of the two nominal genera *Jordanella* and *Garmanella* but preferred to keep them distinct. Since each genus is monotypic, it is in the interest of having generic categories define derived groups, rather than recognize individual differences, that these two genera are synonymized.

MATERIAL EXAMINED: *J. floridae*: Florida: the types as listed above; AMNH 2769 (3); Collier Co. AMNH 22060 (6+); Aquarium material: AMNH 38410SW (3*). *J. pulchra*: Yucatan: Paratypes: USNM 117542 (2); USNM 192329 (1*/19); Belize: FMNH 82343 (1*/3).

### GENUS *CUALAC* MILLER

*Cualac* Miller, 1956, p. 1 (type species *Cualac tessellatus* Miller by original designation).

ETYMOLOGY: *Cualac* derived from a Mexican place name of Nahuatl origin meaning where there is good water (Miller, 1956).

TYPES: Mexico: San Luis Potosi: outlet ditch of La Media Luna, 7 mi. SSW of settlement of Rio Verde: *Cualac tessellatus* Miller, Holotype, UMMZ 17135 (1).

COMPOSITION: Solely the type species.

DIAGNOSIS: Distinguished from all other cyprinodontiform fishes by having closely packed villiform inferior pharyngeal teeth, and from other New World cyprinodontines by an increase in gill rakers on the first arch to 17.

DEFINITION: Anal: (i) 9–10; Dorsal: (i) 9–11; Pelvic: 6–8. Pectoral: 12–13; Caudal: 7, 14, 7; Vertebrae: 14+15; Gill rakers on the anterior arm of the first arch: 14–23. Branchiostegal rays: 5; Scales lateral series: 26–29.

First pleural rib on parapophysis of second vertebra; parapophysis not reduced; no pleural ribs on hemal spines; hypural plates fused into hypural fan. Epipleural ribs not bifid.

Anal fin not modified into a gonopodium; anal fin musculature unmodified; first proximal radial present; middle anal radials present.

Spermatozeugmata not formed; fertilization external; development nonannual; oviparous. Eggs round.

One dorsal ray articulating with the first two dorsal radials; dorsal fin origin opposite origin of anal.

Autopterotic fossa reduced; lateral ethmoid expanded medially, reaching parasphenoid and lying perpendicular to frontal; parasphenoid not expanded anteriorly; no supraoccipital and exoccipital processes; neural arches of first vertebra open and applied to skull; first vertebra articulates with skull via basioccipital condyles; exoccipital condyles absent; supraoccipital included in formation of foramen magnum; parietals absent; nasals expanded medially.

Mesethmoid ossified; medial processes of pelvic fin base and ischial process not reduced; interarcual cartilage reduced, attaches laterally to second pharyngobranchial with a bony flange; pharyngobranchial teeth arranged in discrete rows; basihyal long and narrow; no tooth patches on second and third hypobranchials; teeth on fourth ceratobranchials; dorsal hypohyal absent; anterior extension of anterior ceratohyal ventral to ventral hypohyal; uncinate process on fourth epibranchial articulates with that of third; first epibranchial wide at its base; interhyal ossified; two ossified basibranchials. Vomer with posterior extension ventral to parasphenoid.

Lacrimal flat and broad, carrying a distinct sensory canal; dermosphenotic and preopercular with distinct sensory canal; pectoral girdle lowset; first postcleithrum present; posttemporal with ossified lower limb; posttemporal not fused to supracleithrum.

Vomer ossified, edentulous; medial arm of maxilla straight with pronounced dorsal processes with a groove, nearly meeting in the midline; ventral arms narrow, not abutting rostral cartilage; outer arm robust.

Premaxillary ascending processes narrow and reduced, not tapered posteriorly and not overlapping in the midline; rostral cartilage reduced or absent; outer arm of premaxilla with alveolar process, indented posteriorly to form S-shaped arm. No ligament from the ventral arms of maxillaries to middle of rostral cartilage; no ethmomaxillary ligament; no meniscus between premaxilla and maxilla. Tricuspid, uniserial outer teeth.

Dentary expanded medially, robust; coronoid process on dentary not overlapping with that of articular; retroarticular not elongate. Autopalatine with head angled anteriorly; ventral process elongate reaching quadrate; metapterygoid absent.

Orbital rim free; anterior naris not tubular; supraorbital sensory pores 1–2a, 2b–6a, 6b–7; seven preopercular pores; mandibular and lacrimal pores replaced by neuromasts.

Females and males of equal sizes; all fins rounded or truncate; pigmentation pattern characterized by a lateral band and faint reticulations on the dorsal and anal fins, more pronounced in males.

No fatty predorsal ridge; swimbladder does not extend posteriorly beyond hemal spines.

DISTRIBUTION: San Luis Potosi, Mexico.

REMARKS: *Cualac* was proposed by Miller (1956) as an intermediate between the subfamilies Fundulinae and Cyprinodontinae because it has a rather elongate body form as in the fundulines, and possesses tricuspid outer teeth and the firm attachment of the first vertebra to the skull as in the cyprinodontines. The characters it shares with the cyprinodontines are derived while those it shares with the fundulines are primitive. Therefore, the genus is placed in the tribe Cyprinodontini.

MATERIAL EXAMINED: Mexico: San Luis Potosi: Paratopotypes: SU 50213 (1*/16).

### GENUS *FLORIDICHTHYS* HUBBS

*Floridichthys* Hubbs, 1926, p. 16 (type species *Cyprinodon carpio* Günther, by monotypy).

ETYMOLOGY: *Floridichthys*, after Florida, to which the genus was believed to be endemic.

TYPES: Florida: *Cyprinodon carpio* Günther, Type, BMNH 1855.9.19:821–825 (1).

COMPOSITION: The type divided into three subspecies: *carpio* (Günther), *barbouri* Hubbs and *polymnus* Hubbs.

DIAGNOSIS: Distinguished from all other cyprinodontoids by having an ossified first pharyngobranchial toothplate which bears a patch of teeth.

DEFINITION: Anal: i, 8; Dorsal: ii, 9; Pelvic: 6–7; Pectoral: 18; Caudal: 9, 13, 9; Vertebrae: 10+13; Gill rakers on the anterior arm of the first arch: 9. Branchiostegal rays: 5–6; Scales lateral series: 23–25.

First pleural rib on parapophysis of second vertebra; parapophysis not reduced; no pleural ribs on hemal spines; hypural plates fused into hypural fan. Epipleural ribs not bifid.

Anal fin not modified into a gonopodium; anal fin musculature unmodified; first proximal radial present; middle anal radials present.

Spermatozeugmata not formed; fertilization external; development nonannual; oviparous. Eggs round.

One dorsal ray articulating with the first two dorsal radials; dorsal fin origin opposite origin of anal.

Autopterotic fossa reduced; lateral ethmoid expanded medially, reaching parasphenoid and lying perpendicular to frontal; parasphenoid not expanded anteriorly; no supraoccipital and exoccipital processes; neural arches of first vertebra open and applied to skull; first vertebra articulates with skull via basioccipital condyles; exoccipital condyles absent; supraoccipital included in formation of foramen magnum; parietals absent; nasals expanded medially.

Mesethmoid ossified; medial processes of pelvic fin base and ischial process not reduced; interarcual cartilage reduced, attaches laterally to second pharyngobranchial with a bony flange; pharyngobranchial teeth arranged in discrete rows; basihyal long and narrow; no tooth patches on second and third hypobranchials; teeth on fourth ceratobranchials; dorsal hypohyal absent; anterior extension of anterior ceratohyal ventral to ventral hypohyal; uncinate process on fourth epibranchial articulates with that of third; first epibranchial wide at its base; first epibranchial toothplate with patch of unicuspid teeth; interhyal ossified; two ossified basibranchials. Vomer with posterior extension ventral to parasphenoid.

Lacrimal flat and broad, carrying a distinct sensory canal; dermosphenotic and preopercular with distinct sensory canal; pectoral girdle lowset; first postcleithrum present; posttemporal with ossified lower limb; posttemporal not fused to supracleithrum.

Vomer ossified, edentulous; medial arm of maxilla straight with pronounced dorsal processes with a groove, nearly meeting in the midline; ventral arms narrow, not abutting rostral cartilage; outer arm robust.

Premaxillary ascending processes narrow and reduced, not tapered posteriorly and not overlapping in the midline; rostral cartilage reduced or absent; outer arm of premaxilla with alveolar process, indented posteriorly to form S-shaped arm. No ligament from the ventral arms of maxillaries to middle of rostral cartilage; no ethmomaxillary ligament; no meniscus between premaxilla and maxilla. Tricuspid, uniserial outer teeth.

Dentary expanded medially, robust; coronoid process on dentary not overlapping with that of articular; retroarticular not elongate. Autopalatine with head angled anteriorly; ventral process elongate reaching quadrate; metaperygoid absent.

Orbital rim free; anterior naris not tubular; supraorbital sensory pores 1–7; seven preopercular pores; three mandibular pores; three lacrimal pores.

Females and males of equal sizes or males larger; fins rounded or truncate; pigmentation pattern characterized by a series of golden crossbars.

No fatty predorsal ridge; swimbladder does not extend posteriorly beyond hemal spines.

DISTRIBUTION: Florida and the Yucatan peninsula, south to Honduras.

REMARKS: *Floridichthys* is the only cyprinodontoid to possess an ossified first pharyngobranchial toothplate that also has teeth. A similar but possibly not homologous state occurs in one species of *Cynolebias*.

MATERIAL EXAMINED: Yucatan: the types as listed above; Belize: AMNH 24632 (3); Florida: Key West: AMNH 2610 (1); Sarasota: 17079 (2); no data: AMNH 21908SW (1+/1), AMNH 21905SW (1+/1), AMNH 21907SW (3+/3).

## GENUS *MEGUPSILON* MILLER AND WALTERS

*Megupsilon* Miller and Walters, 1972, p. 2 (type species, *Megupsilon aporus* Miller and Walters, by original designation).

ETYMOLOGY: *Megupsilon* from the Greek *megas,* meaning great, and *upsilon,* the name of the greek letter Y, in reference to the large Y-chromosome in the male.

TYPES: Mexico: Nuevo Leon: El Potosi: *Megupsilon aporus* Miller and Walters, Holotype: UMMZ 189018 (1).

COMPOSITION: Solely the type species.

DIAGNOSIS: Distinguished from all other cyprinodontiform fishes by having an enlarged Y-chromosome in the male; sexually dimorphic chromosome numbers; and a lack of cephalic sensory pores.

DEFINITION: Anal: (0,1) 9–11; Dorsal: 9–11; Pelvic: 0; Pectoral: 13–15; Caudal: 18; Vertebrae: 11–12+13–16. Gill rakers on the anterior arm of the first arch: 8–13; Branchiostegal rays; 5; Scales lateral series: 24–26.

First pleural rib on parapophysis of second vertebra; parapophysis not reduced; no pleural ribs on hemal spines; hypural plates fused into hypural fan. Epipleural ribs not bifid.

Anal fin not modified into a gonopodium; anal fin musculature unmodified; first proximal radial present; middle anal radials present.

Spermatozeugmata not formed; fertilization external; development nonannual; oviparous. Eggs round.

One dorsal ray articulating with the first two dorsal radials; dorsal fin origin opposite origin of anal.

Autopterotic fossa reduced; lateral ethmoid expanded medially, reaching parasphenoid and lying perpendicular to frontal; parasphenoid not expanded anteriorly; no supraoccipital and exoccipital processes; neural arches of first vertebra open and applied to processes; neural arches of first vertebra open and applied to skull; first vertebra articulates with skull via basioccipital condyles; exoccipital condyles absent; supraoccipital included in formation of foramen magnum; parietals absent; nasals expanded medially.

Mesethmoid ossified; pelvic fins and fin supports absent; interarcual cartilage reduced, attaches laterally to second pharyngobranchial with a bony flange; pharyngobranchial teeth arranged in discrete rows; basihyal long and narrow; no tooth patches on second and third hypobranchials; teeth on fourth ceratobranchials; dorsal hypohyal absent; anterior extension of anterior ceratohyal ventral to ventral hypohyal; uncinate process on fourth epibranchial articulates with that of third; first epibranchial wide at its base; interhyal ossified; two ossified basibranchials. Vomer with posterior extension ventral to parasphenoid.

Lacrimal flat and broad, carrying a distinct sensory canal; dermosphenotic and preopercular with a distinct sensory canal; pectoral girdle lowset; first postcleithrum present; posttemporal with ossified lower limb; posttemporal not fused to supracleithrum.

Vomer ossified, edentulous; medial arm of maxilla straight with pronounced dorsal processes with a groove, nearly meeting in the midline; ventral arms narrow, not abutting rostral cartilage; outer arm robust.

Premaxillary ascending processes narrow and reduced, not tapered posteriorly and not overlapping in the midline; rostral cartilage reduced; outer arm of premaxilla with alveolar process, indented posteriorly to form S-shaped arm; No ligament from the ventral arms of maxillaries to middle of rostral cartilage; no ethmomaxillary ligament; no meniscus between premaxilla and maxilla. Tricuspid, uniserial outer teeth.

Dentary expanded medially, robust; coronoid process on dentary not overlapping with that of articular; retroarticular not elongate. Autopalatine with head angled anteriorly; ventral process elongate reaching quadrate; metapterygoid absent.

Orbital rim free; anterior naris not tubular; supraorbital sensory pores absent or replaced by neuromasts; no preopercular pores; no mandibular pores; no lacrimal pores.

Females larger than males; fins rounded or truncate; males with blackened scales on sides of body.

No fatty predorsal ridge; swimbladder does not extend posteriorly beyond hemal spines.

DISTRIBUTION: Nuevo Leon, Mexico.

REMARKS: Meristic data ranges for this genus are supplemented by data from Miller and Walters (1972).

MATERIAL EXAMINED: Mexico: Nuevo Leon, spring-fed pond at Potosi: Paratypes: AMNH 38405 (ex. UMMZ 189020) (2*/10).

# HISTORICAL BIOGEOGRAPHY

Historical distributions of organisms are interpreted traditionally in terms of the identification of a center of origin or dispersal. This is defined as the area of greatest density, or of the location of the most advanced members. Once such a center is chosen, the distribution of a group of organisms may be explained by its dispersal from that center throughout its range (Darlington, 1957). The ability of an organism to disperse a given distance is termed that organism's vagility, and is typically estimated from the observed activity.

Aquatic organisms are supposedly restricted in ability to disperse by their ability to survive in marine, fresh, or brackish waters. Cyprinodontiform fishes have been termed secondary freshwater fishes since many members typically enter brackish water either seasonally or throughout the year. The widespread distribution of the group (fig. 1), therefore, has been explained by dispersalist biogeographers (Myers, 1933a; Kosswig, 1943; Sethi, 1978) as a result of a dispersal from a Mediterranean (Tethys Sea) center of origin during the late Triassic.

One alternative method of biogeographic analysis has been proposed by Hennig (1966) and exemplified for the midges by Brundin (1966). This method, termed the Progression Rule, assumed that the most primitive members of a group occupy the group's center of dispersal, and the more derived members have arrived at their present distribution by dispersing from that center. Although it takes into consideration the phylogeny of a group of organisms, the Progression Rule is essentially a center of origin/dispersal model. It assumes that cladistically apomorph organisms are better at dispersing than their cladistically plesiomorph relatives, a general assumption that is unsupportable.

A third method of analysis has been proposed principally by Croizat and others (Croizat, 1958, 1964; Croizat, Nelson and Rosen, 1974). The method, now alternately termed vicariance or cladistic biogeography (although it was not proposed as such) has as its main premise the idea that the world and its biota evolved together. In striking contrast to both the dispersalist model and the Progression Rule, the aim of vicariance biogeography is to interpret the distribution of a group in terms of its relationship to a general pattern exhibited by all other organisms inhabiting the same area. Dispersalists and Progression Rule biogeographers typically interpret the distribution of a group as if it evolved not only in isolation from other organisms, but with little relation to the geological or geographic history of the earth as well.

Vicariance biogeography as outlined by Croizat and other workers deals with the recognition of tracks of organisms which are defined by the coincident distributions of many groups. A large number of groups sharing the same distribution are logically inferred to have shared an ancestral distribution as outlined by the limits of the biota. The assessment of a dispersal is viewed as a parsimony problem; that is, if there were 10 taxa exhibiting the same distribution and one exhibiting a slightly different one, the unique distribution is postulated to be caused by a dispersal of that taxon away from the rest of the biota (Rosen, 1976).

Vicariance biogeography has been combined with the theories of phylogenetic systematics to become what is termed cladistic biogeography. As outlined by Rosen (1978) and Platnick and Nelson (1978), the aspects of a group to be compared are not solely the distributions of those organisms, but their phylogenies as well.

Introduced into the analysis was the transformation of cladograms of taxa into cladograms of areas, which in turn could be analyzed using the parsimony method. An area is then treated as an area state, and its relation to other area states, as expressed by the phylogeny, are treated as character states in the analysis (Parenti, 1981; Rosen, 1978). Once this is done for seveal groups of organisms with coincident distributions, a pattern of earth history is suggested. The pattern is independent of geological hypotheses; however, a proposed geological model may fit such a pattern. If none is found, this does not necessarily suggest that the phylogeny of these organisms is incorrect, but that the geological models may be inappropriate.

The role of fossils in biogeographic studies has traditionally been as the estimator of the age of origin or earliest time of dispersal into a region (Darlington, 1957). Proponents of the Progression Rule also supported this argument. Vicariance biogeographers have emphasized that a fossil can only give the minimum estimate of the age of a group, and that most groups must be older than their oldest fossil representative.

The precise role fossils play in biogeographic studies has been summarized most recently and debated by Patterson (1981) and Parenti (1981). Patterson concurred with others recently addressing the problem (e.g., Rosen, 1976) that a fossil may be used as an arbiter between dispersal and extinction in lieu of parsimony. For example, if an incongruent distribution was expressed by a group, and such member fossils, then one could know that the fossils represented an ancestral distribution rather than a dispersal. Parenti argued that even though an organism could not have dispersed since the time it was fossilized, previous to that time it could have dispersed as well as any other member of the group; therefore, fossils did not automatically indicate the limits of an ancestral biota unless an estimate of the age of that biota was specified.

GENERAL PATTERN OF CYPRINODONTIFORMS: The present-day distribution of cyprinodontiforms (fig. 1) seems to be an expanded Gondwanian or reduced Pangean pattern with members absent from Australia, Antarctica, and the Orient but present in North America. No members are found east of Wallace's line, a classic line of demarcation in the Indo-Australian region. The distribution is approximated roughly in fishes by the Ostariophysi minus the Oriental cyprinids and Australian plotosids (Nelson, 1976) and the synbranchids minus the Australian and Oriental components (Rosen, 1976).

The pattern is interpreted as Pangean in part based on a reconstruction of the ancient land mass which began its disruption in the late Triassic. An alternative theory of earth history has been advanced by Nur and Ben-Avraham (1977) and Shields (1979) in which another ancient continent, Pacifica, existed until starting to break up during the Jurassic, opening the Pacific for the first time in modern history. Transpacific distributions would support such a theory; however, none exists for cyprinodontiform fishes. That cyprinodontiforms are uninformative with respect to the existence of a Pacific continent could be an indication of a difference in the absolute age of Pacific versus Pangean groups. This suggests that such competing theories of earth history may not be in competition at all, but rather that they explain the distribution of groups that originated at different times.

The late Triassic is given as an estimate of the minimum age of cyprinodontiforms since by that time the Laurasian and Gondwanian land masses had begun their separation. A more precise estimate of a minimum age would be the last time these land masses were still in contact. The late Triassic, therefore, is used as an estimate only until a more precise date can be given.

The oldest described cyprinodont fossil is a species referred to the genus *Prolebias*, an Anatolian cyprinodontine from the Oligocene of Europe (Sauvage, 1874). The distribution of the group, however, supports the contention that cyprinodontiforms could be much older. The oldest fossil does give a minimum age of the group; however, a more reliable indicator is the minimum age of the group's distributional pattern. This may be estimated as the age of the oldest fossil of a group exhibiting the pattern, or, without such evidence, reference to a particular geological pattern. For example, cichlids have a distribution corresponding, in part, to that of the cyprinodontiforms, and their pattern of relationships falls into the same general pattern. Therefore, one could also estimate the age of cichlids as at least the late Triassic. If a fossil of an older age was found for either group, then the minimum age of both groups should be re-estimated at that greater age. This conclusion follows the most par-

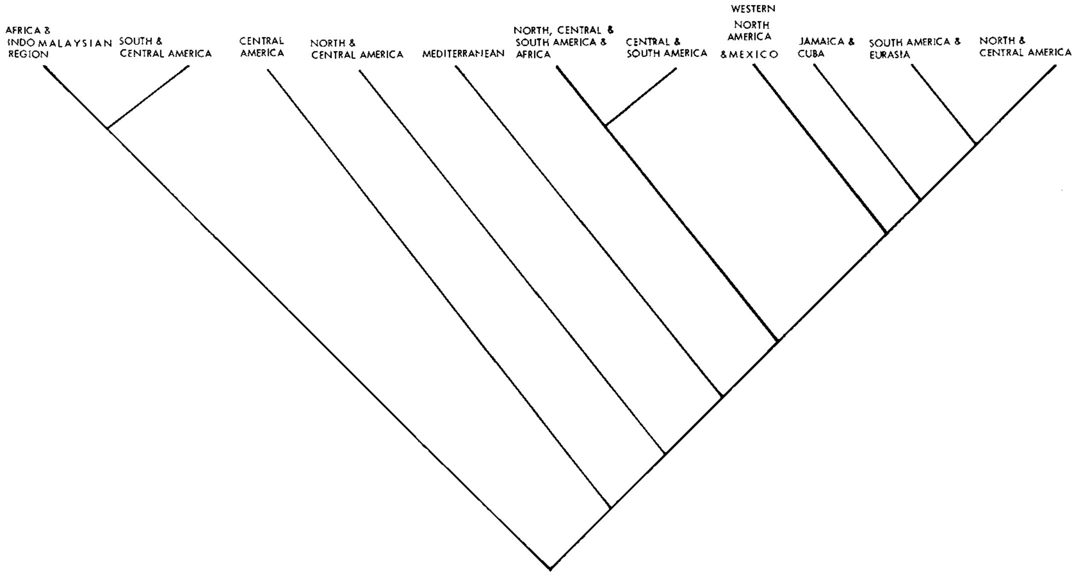

FIG. 90. Cladogram of areas for all cyprinodontiforms (after fig. 9).

simonious assumption; that is, if two groups share a pattern, their history of distribution, and hence age of origin, must correspond (see Parenti, 1981). Also, the oldest fossil is an unreliable indicator of the age of cyprinodontiforms since, were there no fossil record, the estimated minimum age would be the same.

PATTERNS WITHIN CYPRINODONTIFORMS: To describe the association of sister groups with respect to their distribution, it is useful to transform the cladogram of interrelationships (fig. 9) into a cladogram of areas (fig. 90), following the method suggested by Rosen (1978). An association between South America and Africa is repeated twice on the overall cladogram, once corresponding to the distribution of the tropical aplocheiloids, and again corresponding to the distribution of the poeciliids, *Fluviphylax*, procatopines, and *Pantanodon*.

The associations among North, Middle, and South America correspond to those found by Rosen (1976). His North American-Caribbean track is associated with the North American-Central American distributions exhibited by the fundulines; New World cyprinodontines; and *Empetrichthys*, *Crenichthys* and the goodeids. The South American-Caribbean track is associated with the distribution of *Jenynsia*, *Anableps*, and *Oxyzygonectes*, and the Neotropical aplocheiloids. The poeciliids exhibit properties coincident with both patterns (Compare figs. 9 and 90).

The association of Jamaica with Cuba (fig. 90) representing the distribution of the genus *Cubanichthys* does not coincide with distributions on these two Caribbean islands as discussed by Rosen (1976); however, our poor knowledge of relationships of organisms in this region, as well as the sister group relationship of *Cubanichthys* to Old World and New World cyprinodontines and *Orestias*, precludes a conclusion concerning the dispersal of one or the other species of this genus.

The placement of the Mediterranean *Valencia* on the cladogram of cyprinodontiforms indicates the polyphyletic nature of the Eurasian killifishes. *Valencia*, although previously classified as a funduline, has also been referred to the Anatolian cyprinodontines, to both of which it is inferred in this study to have no close relationship.

The aberrant pattern of the general distribution is that expressed by the relationship of the western South American *Orestias* and the Anatolian cyprinodontines.

Previous to this study, the sister group of *Orestias* had been speculated on by several workers including Foster (1967). The southern South American aplocheiloid *Cynolebias* was postulated as its sister group based on apparently derived head pore pattern and osteological similarities. However, it is hypothesized that these similarities represent convergences, and that *Orestias* is most closely related to the Anatolian genus *Kosswigichthys*.

The genus *Orestias* is endemic to the high-altitude lakes of the Andes. Its distribution (fig. 85) was believed (Villwock, 1963) to be restricted to the region between Lake Junin, Peru and northern Chile; however, recent collections of the genus indicate it is distributed much farther north (the known limit Lago Llascha, Peru), thus supporting the idea that it is distributed extensively in the lakes all along the continental divide. The genus has no fossil record.

Anatolian cyprinodontines are currently widely distributed in the Mediterranean region, along the periphery of the Saudi Arabian Peninsula and into Turkey and Iran (fig. 86). Fossils referable to the group are relatively abundant; the oldest is from the Oligocene of Europe.

The extra-continental sister-group relationship of South America-Eurasia is not limited to the *Orestias*-Anatolian group. In the dog family (Canidae) the Eurasian *Nyctereutes* has a hypothesized sister group, the genus *Cerdocyon*, found in the savanna-grasslands of western South America from Venezuela to Paraguay. There is also a possible fossil form referable to *Cerdocyon* in North America (R. H. Tedford, personal commun.). However, the close relationship of *Cerdocyon* to a North American taxon would serve as a refutation of the close relationship of South America to Eurasia. A third set of relationships involving taxa of western South America and a North American-European sister pair was supported by over 10 cladograms of areas (Patterson, 1981), and therefore appears to have some generality.

Is the relationship of South American taxa to North American-European taxa dispersal of such taxa? Such is postulated by Marshall (1979) who, on the basis of geological and radioisotopic as well as fossil plant and animal data, concludes that South American cricetine rodents entered South America 7 Mill. YBP, at least four million years before the presumed formation of the Panamanian landbridge. Therefore, as a dispersalist, Marshall was forced to postulate waif dispersal for the rodents.

Assuming that waif dispersal is possible, any group could have arrived in South America at any time in history, leaving the dispersalist's theory untestable. There are no fossil *Orestias* on which to base such a theory. Time of formation of the Andes, however, provides an estimate of a minimum age of the group, or latest time of dispersal into South America, if that occurred. The uplift of the modern Andes occurred during the period from the Late Jurassic through the Late Cretaceous (Dott and Batten, 1976). The modern Andes were preceded by highlands in western Venezuela, Colombia, Ecuador, and Peru which were a result of uplift and intrusion during the Permo-Triassic. If we assume that *Orestias* was uplifted along with the Andes, then we must conclude they are at least as old as the Late Cretaceous and possibly older if *Orestias* is most closely related to a fish from the Anatolian region.

The Anatolian cyprinodontines have a distribution corresponding to the ancient land connections of Iran and Arabia, Turkey-Greece and North Africa, Italy, Sardinia, Corsica and southern France, and eastern Spain, and northwestern Africa and Spain. The distribution is most simply explained by the break-up of these land masses as the Tethys Sea became obliterated. If *Orestias* is closely related to a member of the group, however, and the distribution is related to earth history at some level, two explanations are possible: (1) there was once a connection between western South America and the Anatolian region, or (2) a monophyletic group

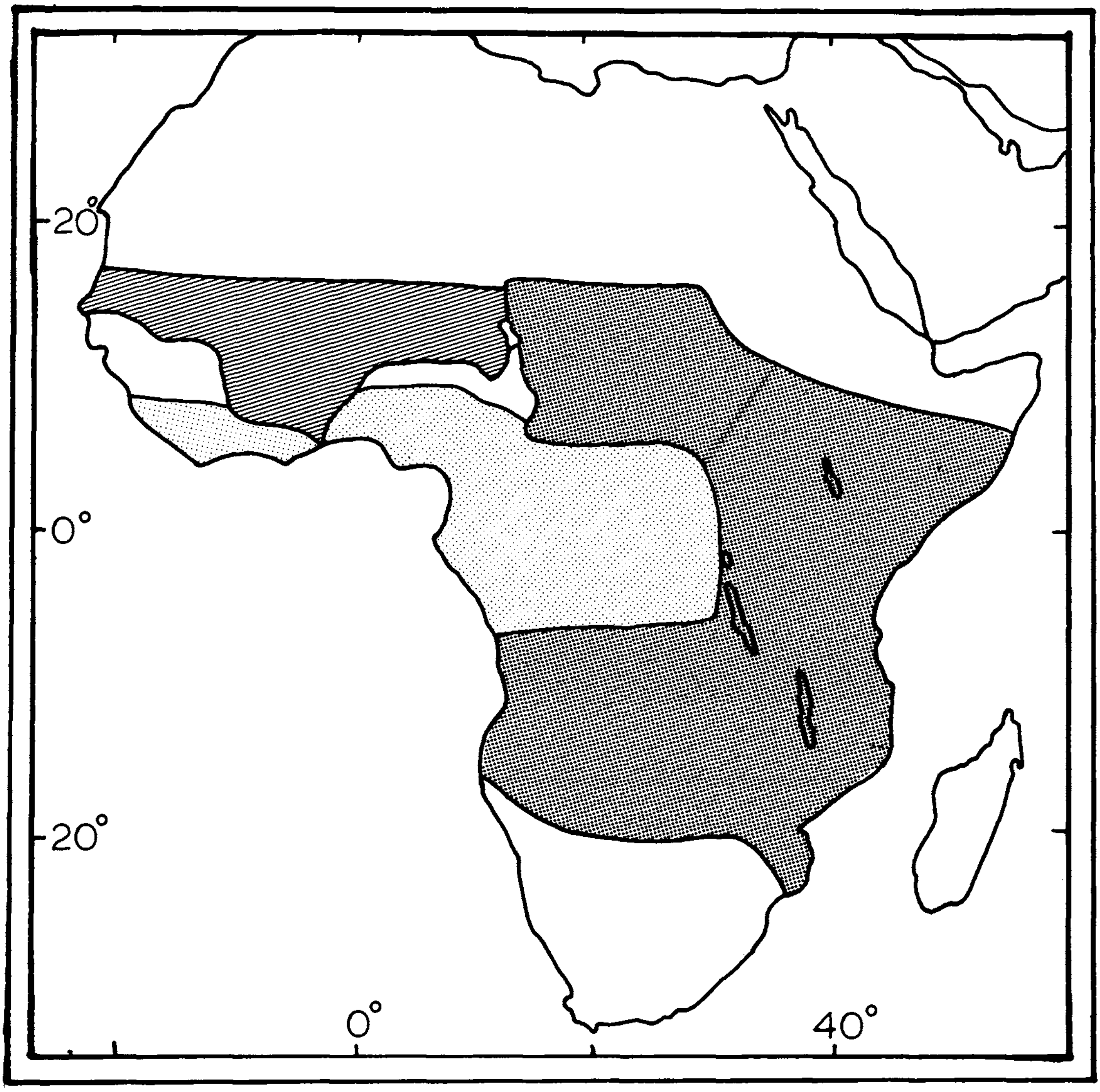

FIG. 91. Distributional limits of *Nothobranchius* and *Aphyosemion*. Darkly stippled area represents the distribution of *Nothobranchius* minus its most plesiomorphic species, *thierryi*. Cross-hatched area represents distribution of *thierryi*. Lightly stippled area represents distribution of *Aphyosemion* (including *Fundulopanchax* as in this study). (After Huber, 1978.)

including *Orestias* and the Anatolian cyprinodontines was once more extensive and has undergone widespread extinction.

Little support exists for the first proposal. The second, however, is supported by the distribution of canids, as well as of plethodontid salamanders (see Rosen, 1976).

This distribution could be interpreted as a dispersal, although the relationship of the land masses today makes such an explanation highly unparsimonious.

We see the pattern as unusual because there is no general explanation for it. Relationships of organisms consistent with a Pan-

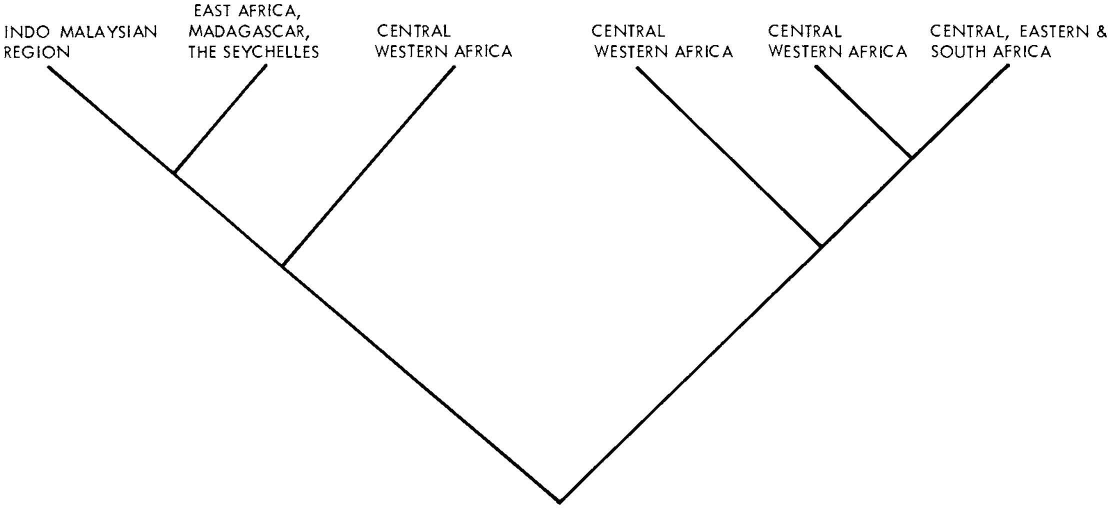

FIG. 92. Cladogram of areas for Old World aplocheiloids (after fig. 25).

gean break-up may not be part of the most general pattern of earth history; however, the only way of discovering this is to discover patterns of distribution that suggest some other explanation of earth history. The Pangean model is not considered an adequate explanation for the historical distribution of cyprinodontiforms for it does not explain satisfactorily the relationship among South America, Eurasia, and North America suggested by cyprinodontiforms, canids, plethodontids, and perhaps many other groups. Current geological hypotheses are uninformative with respect to relationships of such areas.

PATTERNS OF MONOPHYLETIC SUBGROUPS: Within Africa, there is an east-west as well as a north-south dichotomy (fig. 91). *Nothobranchius thierryi* inhabits western Africa, whereas all other *Nothobranchius* species are found in eastern and southern Africa. The same is the case for species of *Aphyosemion,* the most primitive of which are found west of the Dahomey Gap, whereas the more derived members and those more closely related to *Nothobranchius* and referred to the genus *Fundulopanchax* are found in the Congo Basin (fig. 92).

Similarly, Neotropical aplocheiloids (fig. 93) show a repeated north/south South American dichotomy, with typically, but not exclusively, the more derived members of a pair found in southern South America (e.g., as for *Austrofundulus* and *Cynolebias*). Central America is the area plesiomorphic to these two.

Such a pattern is repeated, in part, by *Jenynsia, Anableps,* and *Oxyzygonectes* (fig. 94) in which the plesiomorphic *Oxyzygonectes* inhabits the Pacific coast of Costa Rica, whereas the more derived pair of *Anableps* and *Jenynsia* inhabit Central America and northern South America and southern South America, respectively. *Anableps,* however, is sympatric with *Oxyzygonectes* suggesting a more complicated distributional history within Central America. Poeciliids inhabit all three areas, as well as part of North America. However, the phylogeny of its subgroups has not been worked out.

Given that the associations between South America and Africa are supported twice (figs. 93, 95), resolution of the relationship of *Fluviphylax* as the sister group of either the poeciliids or the procatopines or *Pantanodon* would not produce an astounding biogeographic pattern. Simpson (1977) postulates that the two continental masses began rifting 130 mill. YBP. The final separation of South America and Africa at the equatorial shear zone is estimated at 80 mill YBP, in the Upper Cretaceous. Therefore, estimates

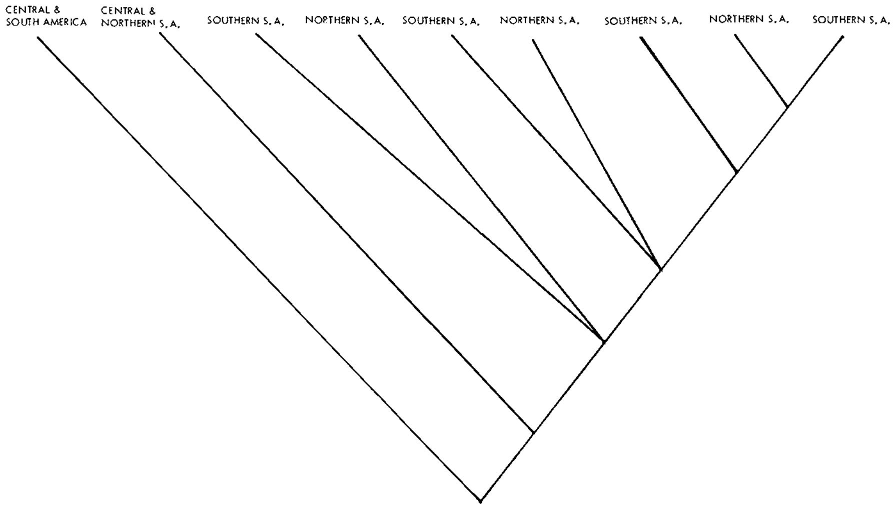

FIG. 93. Cladogram of areas for Neotropical aplocheiloids (after fig. 20).

of the ages of trans-South Atlantic relatives should be no earlier than 80 mill YBP, based on Simpson's hypothesis. Confirmation to some other, older geological hypothesis could support an older estimate, however.

Among the procatopines and *Pantanodon* (fig. 95) several of the associations exhibited by the Old World aplocheiloids are repeated. That is, the close relationship of Madagascar to east Africa, and a split between east and west central Africa. Because procatopines are found in the African Rift lakes the association of these fishes with the poeciliids and *Fluviphylax* of the New World resembles, in part, the distribution of cichlids (Nelson, 1976).

Interrelationships of cyprinodontiform fishes distributed exclusively in North and Central America (including Mexico and the Caribbean) present a particular opportunity for interpretation of the biogeographic patterns previously discussed for these regions. No subfamily listed in table 2 has been disrupted in the new classification more so than the Fundulinae; here, the group is elevated to family rank and restricted to five genera whose interrelationships are summarized in figure 75 and biogeographic associations in figure 96.

A prevalent theory among cyprinodont workers is that *Empetrichthys* of the Death Valley system, and *Crenichthys* of eastern Nevada are closely related to *Fundulus*, which in turn, are close relatives of *Profundulus*. All four genera are postulated to be derived from a funduline "ancestral stock" (Uyeno and Miller, 1962). Since the oldest fossil of New world cyprinodonts is a Miocene specimen referable to the genus *Fundulus* (Lugaski, 1977), all differentation of these genera has been postulated to have occurred since the Miocene (Uyeno and Miller, 1962; Hubbs, Miller and Hubbs, 1974). The conclusion that the Cyprinodontidae is a nonmonophyletic group has led to the examination of other cyprinodontoids as possible close relatives of subgroups of the family. Two results of this study are the present hypotheses that the Mexican goodeids are the closest relatives of *Empetrichthys* and *Crenichthys*, and that *Profundulus* is primitive to all other cyprinodontoids. This necessitates a redefinition of biogeographic patterns and hence a new estimate of the time of differentiation of these genera.

The area cladogram for New World cyprinodontines (fig. 97) simply repeats the close relationship of Floridian and Yucatan-Central American taxa to taxa in central Mexico. The North, Middle, and South American distribution of *Cyprinodon* is uninformative with respect to the three area pat-

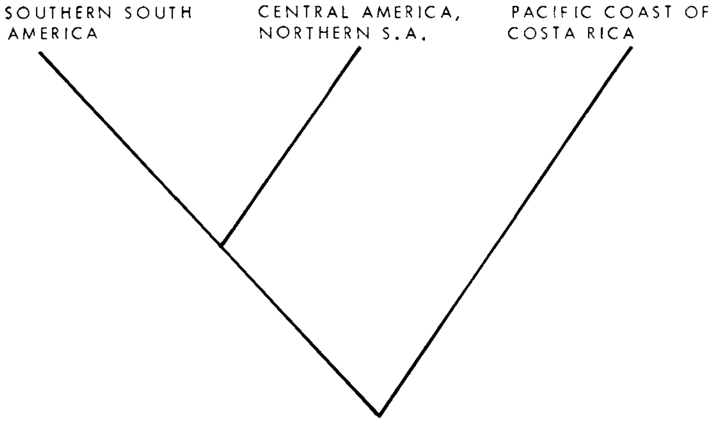

FIG. 94. Cladogram of areas for *Jenynsia, Anableps* and *Oxyzygonectes* (after fig. 79).

tern. However, a subspecies of *C. variegatus,* a species typically found in Florida and along the East Coast of North America, has been described from Yucatan (Hubbs, 1936).

One fossil genus, *Carrionellus* from the Miocene of Ecuador, has been referred to the cyprinodontines. As stated in the systematic section, however, this genus is probably referable to the characoids rather than to the cyprinodontiforms.

Fundulines (fig. 96) share some distribution patterns with the cyprinodontines. Within the genus *Fundulus,* distributed through North and Middle America as well as Bermuda, Cuba, and Hispaniola, there are several species associations between Florida and the Yucatan including the *similis-persimilis* group and the *grandis-grandissimus* group (Miller, 1955b).

*Adinia* and *Leptolucania,* of Florida and coastal regions along the Gulf of Mexico are closely related to *Lucania* of the East Coast of North America and Mexico. The association of Cuba and Florida, supported several times by the distribution of poeciliid species (Rosen and Bailey, 1963) as well as *Rivulus,*

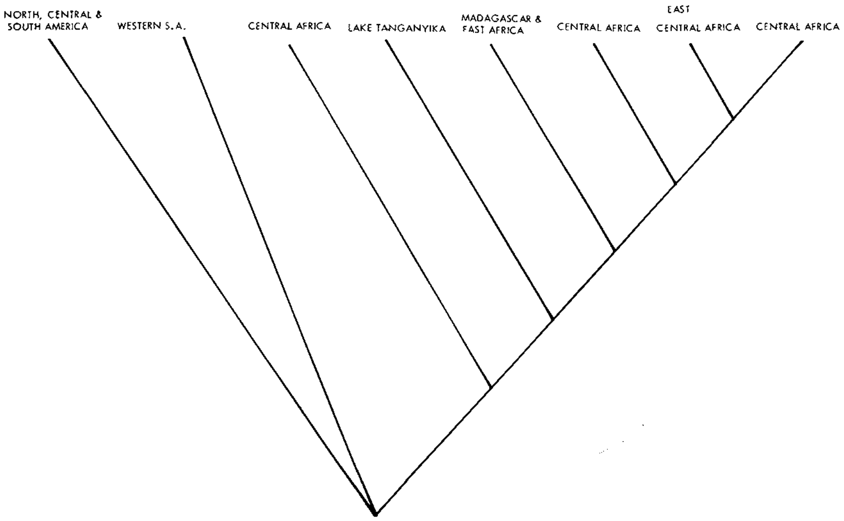

FIG. 95. Cladogram of areas of poeciliids, procatopines, *Fluviphylax* and *Pantanodon* (after fig. 81).

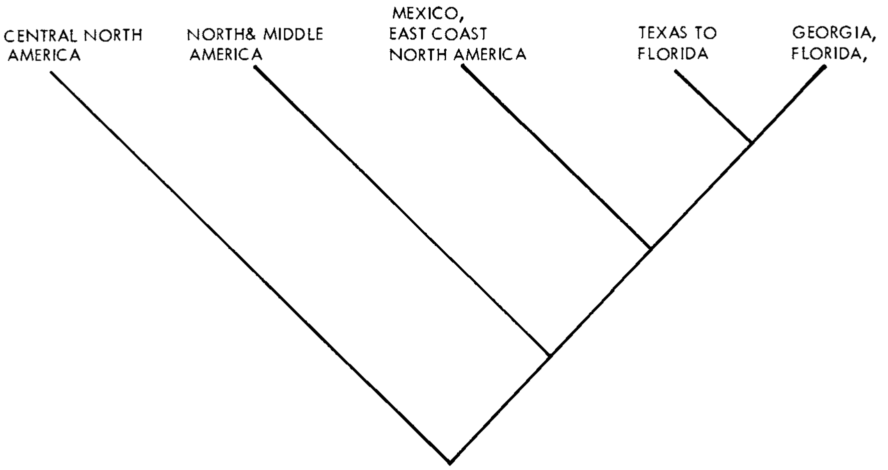

FIG. 96. Cladogram of areas of fundulines (after fig. 75).

is not supported here by *Cubanichthys cubensis* which has no supported close relationships to the Floridian *Lucania goodei,* as suspected by Hubbs and Miller (1965).

Cyprinodontiforms west of the Rocky Mountains are represented by four Recent genera: *Fundulus, Empetrichthys, Crenichthys,* and *Cyprinodon.* [*Lucania* has been introduced into San Francisco Bay and other localities in California, Hubbs and Miller, 1965.] Fossils are referable to the genera *Cyprinodon, Fundulus* and *Empetrichthys* and *Parafundulus* (Miller, 1945; Uyeno and Miller, 1962). As stated, the oldest fossil is Miocene; therefore, differentiation of these genera have been interpreted as resulting from events since the Miocene. However, it is again emphasized that a Miocene fossil presents only a minimum estimate of the age of the group. Therefore, an age estimated by the pattern of interrelationships as correlated with a geologic event will give a more useful

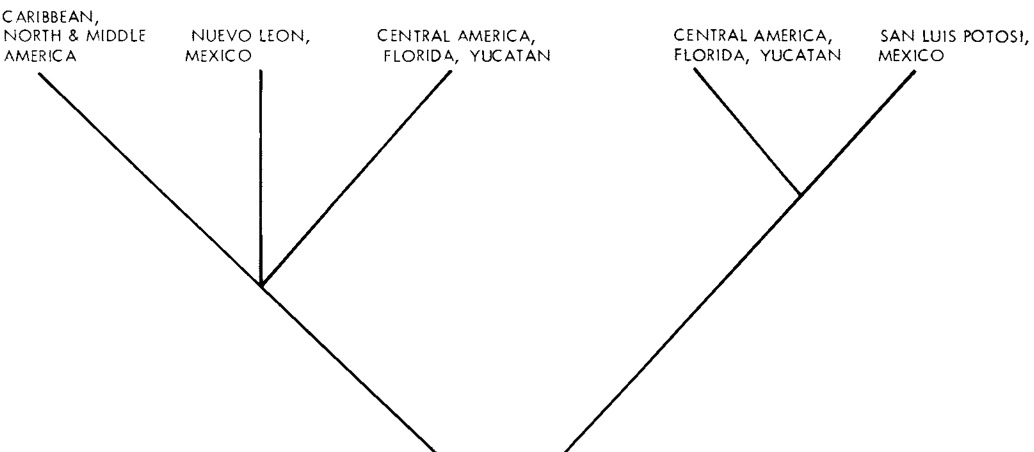

FIG. 97. Cladogram of areas of New World cyprinodontines (after fig. 89).

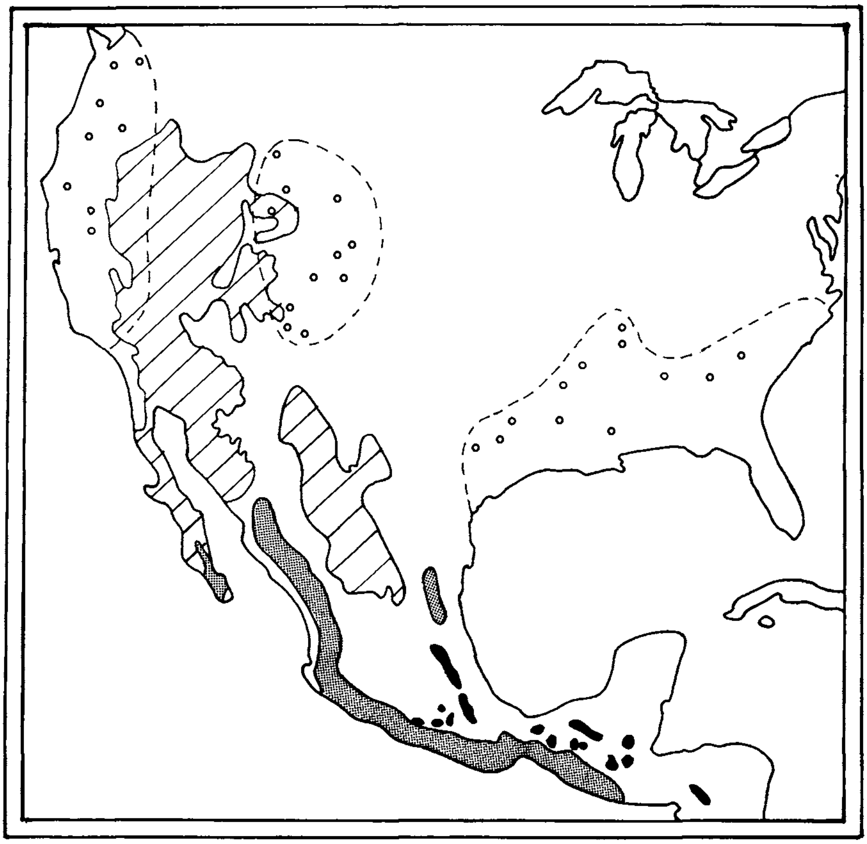

FIG. 98. Fossil affinities across western North and Middle America (after Axelrod, 1979). Open circled denote localities of fossils with affinities in the dry tropic forest (stippled) and temperate rainforest (blackened). Present-day desert regions are cross-hatched.

estimate. The association of *Empetrichthys* and *Crenichthys* with the goodeids of the Mexican Plateau enlarges the area for such an analysis.

Pleistocene and Miocene goodeids (Alvarez and Arreola, 1972; Smith, Miller and Cavender, 1975) allow for an estimate of the Miocene for a minimum age of the ancestral biota of these three taxa.

The two Recent Californian species of *Fundulus, parvipinnis,* and *lima,* the last only of Baja California, are considered to be sister species and in turn most closely related to *diaphanus* of east of the Rocky Mountains (Farris, 1968). Sister group pairs across the Gulf of California, which opened in the Miocene-Pliocene also occur for various groups of desert plants (Axelrod, 1979).

The species of *Cyprinodon,* including the *nevadensis* complex, *diabolis, salinus, radiosus,* and *milleri* are probably most closely related to the *Cyprinodon* species of eastern Mexico.

The age of the regions of the Cordillera inhabited by cyprinodontiforms may be estimated from either a hypothesis of the age of mountain building events, or age of fossils of groups showing similar distributions and interrelationships.

The recent formation of the Cordillera, a result of the Late Jurassic subduction of the Pacific plate, began near the Pacific Coast and then moved eastward. In the Rocky Mountains, evidence points toward a Late Cretaceous, early Cenozoic period of deformation (Dott and Batten, 1976).

The last major epeiric seas of which the maximum transgression occurred about 100 mill. YBP was caused by a worldwide rise in sea-level during the Cretaceous. The earliest uplift of the Mexican Plateau and the highlands of western Guatemala and southern Mexico occurred by the Late Cretaceous. By the early Cenozoic, most of North and Central America was approaching its present-day geological features. Thus, geological evidence does not preclude an age of origin of these cyprinodontiform fishes by Late Cretaceous times.

However, owing to the prevalent marine transgression, support from other organisms is considered almost a prerequisite to pushing back the estimates of latest time of origin of the killifishes. Another group of organisms with a similar distribution and yet much older fossils would help to support a more ancient origin.

Axelrod (1979) has recently summarized the available information on distribution of plants, both fossil and Recent, in western North and Middle America in order to estimate a time of origin of the Sonoran Desert flora. Also summarized were the major floral associations of the other North and Middle American desert regions.

Ancient associations across desert environments, which Axelrod termed links across the desert, led him to conclude that the Sonoran Desert vegetation as well as associated floras throughout the Cordilleran region is as old as the Late Cretaceous and early Tertiary, having originated before modern desert formation.

Distributions of sister-group pairs between California and Arizona-Texas across the desert imply at least a late Eocene-Oligocene connection.

The development of the Sonoran Desert is seen by Axelrod (p. 11) as a: "gradual desiccation during the Tertiary, changing gradually from a well-watered area to the present region of extreme drought." Therefore, the formation of desert regions is inferred to have disrupted larger, more widespread ancestral biotas.

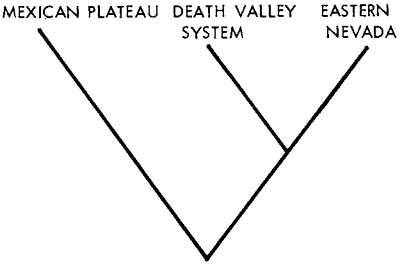

FIG. 99. Cladogram of areas for goodeids, *Empetrichthys*, and *Crenichthys* (after fig. 83).

The flora of western North America is represented by Eocene taxa from central California northward, the Green River and associated areas. These have their closest relatives in the temperate rain and dry tropical forests of Mexico which are not represented by fossils. Fossil taxa of the southeastern United States also have affinities with Recent plants of these regions in Mexico (fig. 98). Thus, an ancient, widespread dicot forest spanning the western Cordilleran from northwestern North America southward into the highlands of Mexico and nuclear Central America existed prior to the late Eocene. Members of this forest included representatives of the dicot genera *Anemia, Ficus, Magnolia* and *Platanus.* Axelrod suggested that the "pathway" for such a connection was the Sierra Madre Occidentale, the eastern range not having been formed by that time.

Disjunct distributions of killifishes across the region are of course supported by the sister group relationship of *Empetrichthys, Crenichthys,* and the goodeids (fig. 99), as well as the *Cyprinodon* and *Fundulus* species, and the genus *Lucania.* One species of *Lucania, interiorus,* occupies the Cuatro Cienegas basin, an aquatic environment centered in the Chihuahuan desert with a diverse fish fauna (Minckley, 1969). Other species inhabit the coastal lowlands of the southeastern United States.

Soltz and Naiman (1978) summarized the

distribution of the cyprinodont fishes of Death Valley with regard to their relationship to the past connections of Pleistocene lakes. The disruption of past aquatic connections across much of the region inhabited by these fishes no doubt produced much of the specific differentiation. However, the postulated sister-group relationship of *Empetrichthys* and *Crenichthys* to the goodeids indicates that generic differentiation among the cyprinodonts of the West is much older.

The distribution of *Empetrichthys, Crenichthys,* and the goodeids corresponds with that of the ancient dicot forest (fig. 98). *Empetrichthys* is limited to the Death Valley system today, whereas *Crenichthys* has a limited distribution in southeastern Nevada (fig. 82). Implied is an early Tertiary formation of the ancestral biota which was disrupted by the formation of deserts, wth an apparent extinction of centrally distributed forms. Desert formation (as well as intrusion by humans) continues to cause the extinction of elements of this once more widespread biota; of the two species and three subspecies of *Empetrichthys* described, all but one have become extinct in modern history.

It could be argued that the distribution of plants has nothing to do with that of fishes or that fishes are much younger than plants, and therefore have distributions with little in common. However, the point taken here is first that the distribution of biotas rather than individual groups of organisms should be investigated in a biogeographic analysis, and second that the minimum age of a group may be estimated by its oldest fossil representative or the oldest fossil of a group which shares the pattern. An early estimate for the age of origin of cyprinodonts of the West is further supported by the assessment of *Profundulus,* distributed on the west coast of southern Mexico and Guatemala, as the most primitive cyprinodontoid. It must be at least as old as the rest of the cyprinodontoids, found througout most of temperate and tropical Africa, North America, and Eurasia, the distribution of which suggests a still older history.

## SUMMARY

The cyprinodontiform fishes, formerly classified in five families, the oviparous Cyprinodontidae and four viviparous families, the Poeciliidae, Jenynsiidae, Anablepidae, and Goodeidae constitute a well-known and widely distributed group of acanthopterygian fishes. This study was carried out with the following six objectives: (1) determine the monophyly of the cyprinodontiforms as a group; (2) determine the monophyly of each of the five families; (3) define the major subgroups of cyprinodontiforms, concentrating on the genera of the family Cyprinodontidae; (4) determine the interrelationships of the subgroups; (5) present a comprehensive classification of the cyprinodontiforms which reflects the interrelationships; and (6) provide a hypothesis for the present-day distribution of the group.

The cyprinodontiforms are a monophyletic group based on their sharing the following derived characters: (1) symmetrical caudal fin, externally rounded or truncate (or with fin extensions) and internally with a single epural opposing a similarly shaped parhypural, with the dorsal and ventral hypural plates symmetrical and separate or fused into an hypural fan; (2) a derived form of the upper jaw, the distinctive feature of which is a two-part alveolar arm on the premaxilla; (3) a derived form of the interarcual cartilage, primitively rodlike and equal in length to the epibranchials, from the base of the first epibranchial to a cartilage of the second pharyngobranchial; (4) first pleural rib arising on the parapophysis of the second vertebra (or rarely the first) rather than the third; (5) a primitively lowset pectoral girdle possessing a large, scale-shaped first postcleithrum; and, (6) a derived reproductive pattern characterized by a long developmental period.

The family Cyprinodontidae previously

comprised oviparous fishes in eight subfamilies which were listed in sequence in classifications giving no hint of interrelationships. One subfamily, the Rivulinae, is hypothesized to be the primitive sister group of all other cyprinodontiforms, both oviparous and viviparous, based on the following derived characters which define all cyprinodontoids as a monophyletic group: (1) two ossified basibranchials, rather than three, in the ventral gill arch skeleton; (2) the loss of the dorsal hypohyal; (3) a reduced interarcual cartilage; (4) an autopalatine with an anterior extension offset to the main axis, and a posterior flange together creating a hammer-shaped head of the autopalatine; (5) extension of the autopalatine ventrally to form an anterior covering of the quadrate; (6) loss of the metapterygoid; (7) premaxilla with a posterior indentation of the alveolar arm forming an S-shaped distal arm; (8) dentary expanded medially to form a robust lower jaw; (9) loss of the first dorsal fin ray resulting in the articulation of the first dorsal fin ray with the first two proximal radials; (10) loss of an ethmomaxillary ligament; (11) loss of a ligament from the interior arms of the maxillaries to the middle of the rostral cartilage; and, (12) loss of a meniscus from between the premaxilla and the maxilla.

The aplocheiloids (Rivulinae) are hypothesized to be a monophyletic group based on their sharing the following uniquely or secondarily derived characters: (1) attached orbital rim; (2) cartilaginous mesethmoid; (3) close-set pelvic fin supports; (4) narrow and twisted lacrimal; (5) broad anterior end of the basihyal; (6) tubular anterior nares; (7) reduced cephalic sensory pore pattern; (8) aspects of the pigmentation pattern; and, tentatively (9) a size dimorphism with males larger than females.

Thus, the cyprinodontiforms are divided into two major subgroups, the aplocheiloids and the cyprinodontoids. In the new classification, the entire group is raised to the rank of an order and these subgroups are classified in the suborders Aplocheiloidei and Cyprinodontoidei, respectively.

Among the aplocheiloids, the Old World genera and the Neotropical genera are each recognized as monophyletic groups. Annualism is therefore not considered a uniquely derived character.

The recognized groups dealt with in this study are summarized in the comprehensive classification as follows:

- Order Cyprinodontiformes Berg, 1940
  - Suborder Aplocheiloidei, new usage
    - Family Aplocheilidae Bleeker, 1860
    - Family Rivulidae Myers, 1925
  - Suborder Cyprinodontoidei, new usage
    - Section 1
      - Family Profundulidae Hoedeman and Bronner, 1951
    - Section 2
      - Division 1
        - Family Fundulidae Jordan and Gilbert, 1882
      - Division 2
        - Sept 1
          - Family Valenciidae, new family
        - Sept 2
          - Superfamily Poecilioidea, new usage
            - Family Anablepidae Garman, 1895
              - Subfamily Anablepinae Garman, 1895
              - Subfamily Oxyzygonectinae, new subfamily
            - Family Poeciliidae Garman, 1895
              - Subfamily Poeciliinae Garman, 1895
              - Subfamily Fluviphylacinae Roberts, 1970
              - Subfamily Aplocheilichthyinae Myers, 1928b
          - Superfamily Cyprinodontoidea, new usage
            - Family Goodeidae Jordan, 1923
              - Subfamily Empetrichthyinae Jordan, Evermann and Clark, 1930
              - Subfamily Goodeinae Jordan, 1923
            - Family Cyprinodontidae Gill, 1865
              - Subfamily Cubanichthyinae, new subfamily
              - Subfamily Cyprinodontinae Gill, 1865
                - Tribe Orestiini Bleeker, 1860
                - Tribe Cyprinodontini Gill, 1865

A combination naming and numbering system of classification is adopted in order to represent most dichotomies while keeping the number of empty categories to a minimum. The adoption of such numbering systems is encouraged in order to represent dichotomies while maintaining certain aspects of traditional classifications and not proliferating a series of rarely used names.

Of the genera included previously in the Fundulinae (table 2) only *Fundulus, Lucania, Adinia, Leptolucania,* and the previously classified subgenus *Plancterus* remain together as a monophyletic group of genera. In addition, (1) *Profundulus* is hypothesized to be the most primitive cyprinodontoid; (2) *Valencia* the sister group of all cyprinodontoids minus *Profundulus* and the fundulines; (3) *Oxyzygonectes* the sister group of *Anableps* and *Jenynsia*; (4) *Chriopeoides* and *Cubanichthys,* now synonyms, a sister group of the more derived cyprinodontines and *Orestias,* and (5) *Empetrichthys* and *Crenichthys* closest relatives of the goodeids.

The four viviparous families are retained as monophyletic groups, each undergoing a change in rank. *Anableps* and *Jenynsia* assessed as sister genera primarily on their shared derived reproductive characters, together with *Oxyzygonectes* comprise the family Anablepidae. Therefore, the family Jenynsiidae is dropped from usage.

The poeciliids are reduced to subfamily rank and included with *Fluviphylax* and the *Pantanodon*-procatopine group in the family Poeciliidae.

The goodeids are similarly reduced to a subfamily and together with *Empetrichthys* and *Crenichthys* comprise the family Goodeidae.

The following conclusions concerning viviparity and internal fertilization are presented: (1) internal fertilization has arisen independently among the cyprinodontiforms at least five times, in *Rivulus, Cynolebias,* poeciliids, goodeids, and *Jenynsia-Anableps*; (2) gonopodia occur independently three times, in *Cynolebias,* poeciliids and *Jenynsia-Anableps*; (3) intrafollicular gestation occurs independently in a derived group of poeciliids and in *Anableps*; and (4) spermatozeugmata are considered independently derived in poeciliids, *Anableps* and goodeids.

Within the classification, the following genera are placed in synonymy:

*Rivulichthys* in *Trigonectes.*
*Simpsonichthys, Campellolebias, Cynopoecilus,* and *Terranotus* in *Cynolebias.*
*Platypanchax* in *Hypsopanchax.*
*Hylopanchax* in *Procatopus.*
*Garmanella* in *Jordanella.*
*Anatolichthys* in *Kosswigichthys.*
*Fundulosoma* in *Nothobranchius.*
*Hubbsichthys* is considered a synonym of *Poecilia.*

An analysis of biogeographic patterns expressed by cyprinodontiform fishes indicates that they are distributed in a manner consistent only in part with the break-up of the ancient supercontinent Pangea. The one sister-group relationship inconsistent with this pattern is that of the Andean *Orestias* and the Eurasian *Kosswigichthys.* This pattern has either been caused by dispersal, extinction, or by the vicariance of an ancient land connection.

Cyprinodonts of western North America have a close relationship with those of Middle America. Correlations with patterns exhibited by ancient plants indicate that there was once a more widespread biota extending from northwestern North America through Central America, the flora of which was characterized by a dicot forest. Disruption of the forest, and hence of the biota, by desert formation caused extinctions throughout much of the range. Fossils across desert give an estimate of the minimum age as the Late Cretaceous–Early Tertiary. Therefore, generic differentiation of cyprinodonts of the West is hypothesized to have begun at least by this period.

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