Osteology and Phylogeny of Oviparous Cyprinodont Fishes (Order Cyprinodontiformes)

By

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INTRODUCTION

The fishes of the order Cyprinodontiformes, primarily distributed throughout the tropical regions of the world and represented by more than five hundred species, provide, through a variety of adaptations to many diverse modes of life, a wealth of material for evolutionary and phylogenetic investigation. As a consequence, these fishes have received much attention, especially in matters of taxonomic significance, but practically none of these efforts have been directed toward developing a knowledge of their osteology despite the recognized value of this resource in providing dependable indications of phyletic relationships.

The order is usually divided into two suborders, the Amblyopsoidea and the Poecilioidea, the former containing a few, mostly blind, cave fishes of the central and eastern United States, and the latter including all the other cyprinodonts. Further, the suborder Poecilioidea is subdivided into two superfamilies, one containing the viviparous and the other containing the oviparous forms. In the viviparous superfamily, the structural modifications of the male gonopodium have served to delineate successfully the evolutionary lines of descent but in the oviparous superfamily no such handy taxonomic device is available. This lack of a ready means of analysis not only may be responsible for much of the current uncertainty and controversy relative to the establishment of subordinal taxa for the oviparous representatives but also surely leaves this group without means for analytical comparison with the viviparous members of the order.

The present study was directed to the discovery of osteological information on cyprinodonts through examination and analysis of the skeletal characteristics of selected representatives of the oviparous species. It was anticipated that such a study would both reveal and substantiate major phylogenetic relationships and evolutionary trends peculiar to these fishes, and that it also would provide an osteological foundation for a future, and similar, treatment of the viviparous forms. The completion of such studies should provide for the oviparous and the viviparous groups a sufficiency of shared characteristics to permit analysis of their interrelationships. The necessity for such an evaluation is indicated by the recognized possibility that viviparity may have evolved independently in cyrpinodonts on more than one occasion and that, until this question is resolved, the division of the order into oviparous and viviparous superfamilies must remain a tentative arrangement of convenience.

As a result of the basic needs evident in the cyprinodonts, this study has been restricted to osteological considerations but this limitation in no way lessens the necessity for other anatomical, embryological, ecological, physiological, genetic, behavioral, and zoogeographic studies which will be necessary to the solutions of various problems of relationships and evolution within this extremely interesting group of fishes.

Properly evaluated osteological characters are known to provide dependable evidence of phyletic relationships among the vertebrates and, consequently, the osteology of the several vertebrate groups has been exploited for this purpose. In the case of the fishes, Regan (1909) presented extensive osteological evidence in support of his classification of the teleosts and thereby established a pattern which has been the basis of all subsequent major classifications of the fishes.

Despite the widespread recognition of its importance, the osteology of many fish groups has received only superficial attention and much study remains to be done before our knowledge of the relationships of these groups will be complete. In this connection, the following remarks of Jordan and Evermann (1896: 623) are still pertinent: "While our knowledge of the osteology and embryology of most of the families of fishes is very incomplete, it is evident that the relationships of the groups cannot be shown in any linear series, or by any conceivable arrangement of orders and suborders. The living teleost fishes have sprung from many lines of descent, their relationships are extremely diverse, and their differences are of every possible degree of value. The ordinary schemes have magnified the importance of a few common characters, at the same time neglecting other differences of equal importance. No system of arrangement which throws these fishes into large groups can ever be definite or permanent."

Taxonomic Background

The osteology of the cyprinodonts has not been studied in sufficient detail to permit a satisfactory analysis. As a result, the taxonomic history of the cyprinodonts has culminated in a system of classification which, although useful, is considered unsatisfactory and inconclusive by most current authorities. The root of the difficulty is vested in the consistent selection of characteristics having questionable value in the appraisal of higher categories. A review of the efforts and the thinking along these lines will be informative by specifying the characteristics employed and by pointing out the difficulties and contradictions which they engender.

In the past the group has been confused first with the cyprinids and later with the Haplomi because of superficial rather than genetic resemblance. However, it soon became clear that the cyprinodonts have no close affinity with the cyprinids but their relationship with the Haplomi was not questioned until 1909 when Regan raised the issue.

Prior to Regan's contribution, much emphasis was placed on highly variable nutritional and external characteristics. Using such characters, Gill (1872) grouped together the Esocidae, Umbridae and Cyprinodontidae under Cyprinodontoidea which is equivalent to the Cyprinodontidae of Gunther (1880) and subsequent authors. Jordan and Evermann(1896) grouped Umbridae (Umbra), Lucidae (Esox), Poeciliidae, and Amblyopsidae under Haplomi while Boulenger (1904) included Esocidae, Dalliidae, Cyprinodontidae, Amblyopsidae and ten other families of fishes in the group Haplomi. Regan (1909, 1911), however, restricted Haplomi to include Esocidae, Umbridae and Dalliidae, removed the other ten families to different orders, and proposed the ordinal name Microcyprini to include Cyprinodontidae and Amblyopsidae.

At the same time Regan (1911) proposed a classification of the Microcyprini and listed the ostelogical characters for the group. He pointed out that, whereas the Haplomi showed relationship to the most generalized isospondylous fishes (Clupea, Herengus, etc.), the Microcyprini were more closely related to the acanthopterygians (spiny-rayed fishes). Hubbs (1924) pointed out that the cyprinodonts approach the acanthopterygians in several fundamental characteristics.

The classification of the order Cyprinodontiformes is complicated and has undergone repeated changes. Many of the changes were due to the recurrent and persistent attempts of authors to make use of such highly adaptive and nutrition related characters as the length of the intestine and the shape and arrangement of the teeth. Such characters are now known to have been repeatedly and independently altered in the different lines of evolution within the group. Gunther (1880) employed nutritional characters when he subdivided the Cyprinodontidae into two groups, Cyprinodontidae carnivorae and the Cyprinodontidae limnophagae. Similarly Garman (1895) in his monumental work on the cyprinodonts made use of tooth differences for the primary division of the group. Although such characters were later found to be misleading at this level of classification, they may be employed successfully to separate terminal elements formed by one or a few genera. In addition, these adaptive characters at times may be used for grouping genera into larger natural categories provided they are employed in combination with comparatively conservative characters which provide more reliable indication of relationship.

The classification of the order Cyprinodontiformes as proposed by Regan (1911) has been considerably amended and elaborated upon by several workers, but primarily the revisionary work has been done by Hubbs (1924, 1926, 1936 and 1950) and Myers (1925, 1927, 1928a, 1928b, 1931, 1932, 1933, 1935a, 1935b, 1936, 1938 and 1942). The papers dealing with these contributions are scattered in various journals and several of them are not readily available. For this reason, an outline of the classification currently in use is presented here for reference purposes:

Order: Cyprinodontiformes (Cyprinodontes Agassiz, Microcyprini Regan,
    Cyprinodontida)[1]
  Suborder: Amblyopsoidea
    Family: Amblyopsidae
      Genera: Chologaster Agassiz
        Amblyopsis Dekay
        Typhlichthys Girard
  Suborder: Poecilioidea
    Family: Cyprinodontidae

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[1] Ordinal name as recommended by the committee on fish classification, pp. 326-327 of Copeia, 1950 and by Bailey, 1952.

Subfamily: Fundulinae

Tribe: Fundulini

Genera: <u>Profundulus</u> Hubbs

<u>Empetrichthys</u> Gilbert

<u>Crenichthys</u> Hubbs

<u>Fundulus</u> Lacepede

<u>Adinia</u> Girard

<u>Lucania</u> Girard

<u>Leptolucania</u> Myers

<u>Chriopeops</u> Fowler

<u>Cubanichthys</u> Hubbs

<u>Oxyzygonectes</u> Fowler

<u>Chriopeoides</u> Fowler

<u>Valencia</u> Myers

Tribe: Aplocheilini (Rivulini)[2]

Genera: <u>Aplocheilus</u> McClelland

<u>Epiplatys</u> Gill

<u>Aphyosemion</u> Myers

<u>Nothobranchius</u> Peters

<u>Pachypanchax</u> Myers

<u>Hubbsichthys</u> Schultz

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[2] Myers (1938) in a footnote on p. 137, pointed out that the tribe Rivulini (1931) should be called Aplocheilini, and that Aplocheilini should be known as Oryziatini.

Tribe: Aplocheilini (Rivulini)--Continued

Genera: *Rivulus* Poey
Cynolebias Steindachner
Rachovia Myers
Pterolebias Garman
Rivulichthys Myers
Neofundulus Myers
Trigonectes Myers
Austrofundulus Myers

Tribe: Aplocheilichthyini

Genera: *Procatopus* Boulenger
Hypsopanchax Myers
Platypanchax Ahl
Aplocheilichthys Bleeker
Micropanchax Myers
Cynopanchax Ahl
Plataplocheilus Ahl

Tribe: Oryziatini

Genus: *Oryzias* Jordan and Snyder

Subfamily: Lamprichthyinae

Genus: *Lamprichthys* Regan

Subfamily: Orestiatinae

Genus: *Orestias* Cuvier and Valenciennes

Subfamily: Cyprinodontinae

Genera: Cyprinodon Lacepede

Floridichthys Hubbs

Jordanella Goode and Bean

Garmanella Hubbs

Cualac Miller

Anatolichthys Kosswig and Sozer

Kosswigichthys Sozer

Aphanius Nardo

Aphaniops Hoedeman

Family: Goodeidae

Subfamily: Ataeniobinae

Genus: Ataeniobius Hubbs and Turner

Subfamily: Goodeinae

Genera: Allophorus Hubbs and Turner

Xenotoca Hubbs and Turner

Chapalichthys Meek

Goodea Jordan

Zoogoneticus Meek

Allodontichthys Hubbs and Turner

Neophorous Hubbs and Turner

Xenophorus Hubbs and Turner

Allotoca Hubbs and Turner

Subfamily: Characodontinae

Genus: Characodon Gunther

Subfamily: Girardinichthyinae

- Genera: <u>Ilyodon</u> Eigenmann
  - <u>Balsadichthys</u> Hubbs
  - <u>Girarinichthys</u> Bleeker
  - <u>Lermichthys</u> Hubbs
  - <u>Sikiffia</u> Meek
  - <u>Ollentodon</u> Hubbs and Turner
  - <u>Neotoca</u> Hubbs and Turner

Family: Jenynsiidae

- Genus: <u>Jenynsia</u> Gunther

Family: Poeciliidae

Subfamily: Gambusiinae

Tribe: Gambusiini

- Genera: <u>Heterophallus</u> Regan
  - <u>Gambusia</u> Poey
  - <u>Belonesox</u> Kner

Tribe: Hetarandriini

- Genera: <u>Brachyrhaphis</u> Regan
  - <u>Trigonophallus</u> Hubbs
  - <u>Priapichthys</u> Regan
  - <u>Panamichthys</u> Regan
  - <u>Pseudoxiphophorus</u> Bleeker
  - <u>Heterandria</u> Agassiz
  - <u>Priapella</u> Regan

Tribe: Hetarandriini--Continued

Genera: Allogambusia Hubbs
- Alloheterandria Hubbs
- Neoheterandria Henn
- Pseudopoecilia Regan

Tribe: Quintanini

Genus: Quintana Hubbs

Tribe: Girardinini

Genera: Girardinus Poey
- Toxus Eigenmann
- Glaridichthys Garmann
- Allodontium Howell-Rivero and Rivas
- Dactylophallus Howell-Rivero and Rivas

Tribe: Cnesterodontini

Genera: Cnesterodon Garman
- Darienichtys Hubbs
- Diphyacantha Henn
- Phallocerus Eigenmann
- Phallotorynus Henn

Subfamily: Poeciliopsinae

Genera: Poecilistes Hubbs
- Poeciliopsis Regan
- Aulophallus Hubbs
- Phallichthys Hubbs

Subfamily: Poeciliopsinae--Continued

Genera: Carlhubbsia Whitley

Phalloptychus Eigenmann

Xenophallus Hubbs

Subfamily: Xenodexiinae

Genus: Xenodexia Hubbs

Subfamily: Poeciliinae

Tribe: Poeciliini

Genera: Poecilia Bloch and Schneider

Micropoecilia Hubbs

Limia Poey

Parapoecilia Hubbs

Lebistes Filipi

Allopeocilia Hubbs

Mollienesia LeSueur

Tribe: Xiphophorini

Genus: Xiphophorus Haekel

Tribe: Pamphorini

Genera: Pamphorichthys Regan

Pamphoria Regan

Subfamily: Alfarinae

Genera: Furcipenis Hubbs

Alfaro Meek

Subfamily: Tomeurinae

Genus: Tomeurus Eigenmann

Family: Adrianichthyidae

Genera: *Xenopoecilus* Regan

Adrianichthys M. Weber

Family: Horaichthyidae

Genus: *Horaichthys* Kulkarni

It is pertinent here to mention some of the attempts to make the organization of the families of the order Cyprinodontiformes as natural as possible. Such a consideration will show that classifications based on a single character are often untenable, and that this is especially true when the characters involved happen to be adaptive.

Woods and Inger (1957) grouped the five recognized species of amblyopsids into three genera, *Chologaster*, *Amblyopsis* and *Typhlichthys*, and in the process they synonymized *Troglichthys* Eigenmann with *Amblyopsis* DeKay from which the former differed mainly in the absence of pelvics. In this connection they (1957: 243) maintained that little significance could be attached to the pelvics because of their extreme variability in *Amblyopsis spelaea*.

Regan (1913) published a revision of the subfamily Poeciliinae (Poeciliidae of Hubbs and subsequent authors) on the basis of gonopodial structure. Since then the structure and the arrangement of the terminal elements of the gonopodium of the poeciliid fishes have been used widely in the systematic arrangements of the genera and species. Regan's classification of the poeciliid fishes has subsequently undergone considerable revision by Hubbs (1924, 1926, 1936), Howell-Rivero and Hubbs (1936), Howell-Rivero and Rivas (1944), Hubbs (1950), Gordon and Rosen (1951), Rosen (1952) and Rosen and Gordon (1953).

The subfamily Tomeurinae, which contains a single genus Tomeurus from South America was confused with the Poeciliidae but is now known to be an oviparous form. Moreover, Tomeurus shows certain striking superficial resemblances to the Indian genus Horaichthys, and Hubbs (1941: 447) in commenting upon the relationships of these two genera concluded that they ". . . arose independently from the cyprinodont groups that are respectively characteristic of the two regions." Both Hubbs and Myers (Kulkarni, 1940: 384) have suggested that the subfamily Tomeurinae be raised to a family level. Concerning the placement of Tomeurus and Horaichthys in two separate families, Hubbs, in a letter written to Hora and published by Kulkarni (1940: 384), remarked: "To do this would emphasize the remarkable example of convergent evolution which is involved." More recently Rosen (1953: 3) also has suggested that the subfamily Tomeurinae be raised to a family level.

Kulkarni (1940), therefore, established the new family Horaichthyidae to receive Horaichthys setnai and showed the species to be closely related to Oryzias. Both Hubbs and Myers have expressed agreement with this action (Kulkarni, 1940, 1948; and Hubbs, 1941).

The family Goodeidae has been revised by Hubbs and Turner (1939). The characters used in the revision relate to the structure of the ovary in adult and half grown females and to attributes of the rectal processes of the embryos. Earlier attempts at the classification of this family by Jordan and Everman(1896), Meek (1904), Regan (1906), Jordan (1923) and Hubbs (1924, 1926) were based on dental and intestinal characteristics. These characters, however, were shown to be untenable by Hubbs and Turner (op. cit.) who also established that not only do the characters related to nutrition show intergradation when a large series of forms are compared but also, and more significantly, the classification so derived does not conform to the evident lines of phyletic relationship. The new characters, however, have their limitations in that they can be used with certainty only for adult or nearly adult females. This complicates and hinders the final classification of species known only from males. In this connection Hubbs and Turner (op. cit.: 23) remarked: "The important point is that these characters are the ones indicating the natural groups, and that classifications surely should be made natural rather than convenient."

Each of the two families Jenynsiidae and the Anablepidae contain one genus, Jenynsia and Anableps respectively. Hubbs (1924) pointed out that the latter group might have been derived from the former. He (op. cit.: 4) therefore proposed for each a subfamily status under a single family, Anablepidae. In any case, the two groups might be taken to be closely related. According to Myers (1931) the family Jenynsiidae differs from the aberrant Anablepidae in considerably lesser number of vertebrae, less depressed skull, presence of postcleithera, naked intromittent organ, and normal eyes.

The family Adrianichthyidae is not well known. Weber and Beufort (1923) reviewed the described species. These seem to be confined to the lakes of Celebes and but a few specimens have been found. Myers (1931) pointed out that they differ considerably from the other families and may be viviparous.

The Phallostethidae, small fishes from the Malayan region and externally somewhat resembling the cyprinodonts, have been shown by Myers (1928a) to be not even members of the order Cyprinodontiformes. Berg (1947) placed these fishes in a separate order Phallostethiformes indicating them to be related to Cyprinodontiformes but manifesting a further step toward Perciformes (Acanthopterygii).

The remaining family, Cyprinodontidae, the subject of the present study, is the largest and the most widespread of the order Cyprinodontiformes. The family contains more than three hundred species of similar fishes which unfortunately possess no such ready index of relationship as that provided by the gonopodium of the Poeciliidae. The older attempts at generic segregation were based mainly on a few external differences which collapse completely as characters when large series of species are compared.

Regan (1911) indicated some fundamental differences between _Aplocheilus_ and _Panchax_ which were elaborated upon by Sundra Raj (1916). Ahl (1924, 1928) attempted a classification of the Old World genera, placing much reliance on the differences in dentition. Myers (1925, 1927, 1928a, 1928b, 1931, 1932, 1933, 1935a, 1935b, 1936, 1938, 1942, 1952), in a similar attempt at the classification of the oviparous cyprinodonts, disagreed with Ahl (*op. cit.*) on many points. One of his papers was devoted to a delineation of the primary groups of the oviparous genera and forms a key to the general classification of the oviparous cyprinodonts (Myers, 1931).

The classification of the family Cyprinodontidae, however, still remains a controversial issue among ichthyologists. Since 1931, when Myers published a general classification of this group, a number of new forms have been described. The discovery of the two genera *Crenichthys* Hubbs and *Cualac* Miller have aroused doubts as to the desirability of recognizing two separate subfamilies, Cyprinodontinae and Fundulinae, on the basis of differences in teeth alone. The other two subfamilies, Orestiatinae and Lamprichthyinae, contain a single genus each, and the latter only one species, *Lamprichthys tanganicanus* from Lake Tanganyika. The genus *Orestias*, however, has speciated into a number of forms in Lake Titicaca in the high Andes in Peru (Tchernavin, 1944).

Miller (1955: 9-10) pointed out that the characters listed by Myers (1931) as diagnostic of the subfamily Fundulinae were not applicable in many cases, e.g., *Profundulus*, *Austrofundulus* and many species of *Fundulus*. Therefore he suggested that Myers' (*op. cit.*) diagnosis of the subfamily Fundulinae should be modified in two particulars: (1) there are more than 34 vertebrae, for *Profundulus* has as many as 39, at least eight species of *Fundulus* have as many as 37, and two species of that genus *F. stellifer* (Jordan) and *F. seminolis* Girard, have up to 38 (Garman 1895: 105, 108; Clotheir 1950: 41; Miller 1955: 9-10); and (2) the caudal fin is scaled more than half way to the tip in some species of Profundulus, e.g., P. guatemalensis. This is also true of at least one species of Austrofundulus as pointed out by Myers (1932: 160, and 1942: 112, Fig. 15). Further, the teeth of the Fundulinae, although typically conical, may be bicuspid as in Crenichthys. Therefore, Miller (1955) suggested that the subfamily Cyprinodontinae might be combined in a single subfamily along with the subfamily Fundulinae. In such a case, this single subfamily would be described as having conical, bicuspid, or tricuspid teeth. Moreover, as further pointed out by Miller (1955: 9), Carionellus, described from Ecuador by White (1927), has tricuspid teeth, but otherwise looks like a funduline. Miller (1955) then pointed out that on further study, Carionellus may prove to bridge the small gap currently used to separate the Cyprinodontinae and the Fundulinae. Again, while discussing the relationships of Cualac tessellatus, Miller (1956) discussed the same problem and proposed to unite the two subfamilies into one subfamily Cyrpinodontinae. In this connection he (1956: 5) surmized that "Cualac may well be as closely related to Fundulus, with conical teeth, as to the Cyprinodontids, with tricuspid teeth," and cautioned that (1956: 8) "To base higher classification solely or largely on dental features may be misleading, as it surely was in the diversified Mexican fishes of the family Goodeidae." However, this recognition of one subfamily instead of two was proposed as a tentative arrangement as Miller (1956: 9) himself pointed out.

Hoedeman and Bronner (1951) and Hoedeman (1954) have proposed many changes in Myers' (1931) classification. One such change, the erection of the tribe Profundulidae (Hoedeman and Bronner, 1951) to include Profundulus and Adinia, and the Old World genera Valencia and Kosswigichthys, has been debated with vigor by Miller (1955: 10-11) who regarded it to be an unnatural assemblage and suggested its abandonment.

In view of the above considerations it was evident that the classification of the family Cyprinodontidae was in need of a reexamination based upon as many criteria as possible. Since, moreover, our knowledge of the precise relationships of the numerous genera, especially the fossil ones, is inadequate, it was felt that a thorough knowledge of their osteology was essential to a satisfactory attempt at their classification.

In the absence of such comparative structures as the gonopodia of viviparous poeciliids, the relationships of the oviparous cyprinodonts must be based on other comparative characters. Comparative osteology, as has already been pointed out, affords a valuable clue to relationships. Such a study, however, has been entirely neglected for the cyprinodonts except for a few limited attempts by Ramaswami (1945, 1946) and Kulkarni (1948). Ramaswami (op. cit.), however, did not have phylogenetic considerations in mind when he selected more or less unrelated genera for comparison. Kulkarni (op. cit.) on the other hand, compared the head skeletons of the three genera of Indian cyprinodonts and reached certain important conclusions when he (op. cit.: 103) observed that: "A comparison of the various skeletal features of the three Indian Cyprinodonts studied reveals greater affinity between

H. [oraichthys] setani and O. [ryzias] melastigma than between A. [plocheilus] lineatus and O. [ryzias] melastigma and finally substantiates the view held previously by the author that H. [oraichthys] setani must have evolved directly from O. [ryzias] melastigma."

Hubbs (1924) pointed out that Profundulus, of all American genera, diverges least from a general ancestral type. More recently, however, Myers (1958) commented that instead the oriental genus Aplocheilus presents by far the largest number of basic characters that have become specialized or even lost in other members of the family. As the present study progressed and other genera allied to Aplocheilus were examined, it became clear that both of these above views were in need of re-evaluation.

The geographical distribution of the order Cyprinodontiformes and especially the family Cyprinodontidae presents problems of interest to the student of biogeography. The cyprinodonts are chiefly a freshwater group. Therefore, next to the Ostariophysi, a wholly freshwater group, it should yield data of considerable zoographical significance. It was thought that these and similar problems would be capable of interpretation once the interrelationships of these fishes were known.

Materials and Methods

This study is based upon specimens some of which were collected locally while others were obtained from various institutions. The abbreviations used in reference to collections follow:

ANSP, Academy of Natural Sciences, Philadelphia
BMNH, British Museum of Natural History
CAS, California Academy of Sciences
RPS, Private Collection, R. P. Sethi
RU, Rhodes University, Grahamstown, South Africa
TU, Tulane University
UF, University of Florida
UT, University of Texas
UMMZ, University of Michigan, Museum of Zoology
USNM, United States National Museum
ZMA, Zoologisch Museum, Amsterdam
ZSZM, Zoologisches Staatsinstitut und Zoologisches Museum, Hamburg

Materials

A list of cleared and stained specimens used in this study is given below:

Cyprinodon variegatus variegatus

23 Cedar Key, Fla. (RPS)

Cyprinodon macularius

2 Salton Sea, Calif. (UMMZ 133169)

Cyprinodon salinus

2 Soda Lake, Calif. (UMMZ 172291)

Jordanella floridae

23 near Cedar Key, Fla. (RPS)

Floridichthys carpio carpio

10 Cedar Key, Fla. (RPS)

Cualac tessellatus

5 La Media Luna, San Luis Potosi, Mexico (UMMZ 171136)

Garmanella pulchra

5 Cienega, Yucatan, Mexico (UMMZ 143097)

Fundulus chrysotus

6 near Cedar Key, Fla. (RPS); 6 Gainesville, Fla. (RPS)

Fundulus grandis

5 Cedar Key, Fla. (RPS)

Fundulus similis

4 Cedar Key, Fla. (UF 3103)

Fundulus confluentus

6 Bayport, Fla. (UF 3126)

Fundulus notti

4 Hawthorne Prairie, Marion County, Fla. (UF uncat.)

Fundulus cingulatus

6 near Baxter, Baker County, Fla. (UF 1825)

Fundulus olivaceus

4 Robbers Cave State Park, Okla. (UF 7915)

Fundulus kansae

2 Boonsboro, Missouri (UMMZ 170950)

Adinia xenica

15 Cedar Key, Fla. (RPS)

Lucania parva

18 Cedar Key, Fla. (RPS)

Chriopeops goodei

6 Bayport, Fla. (UF 389)

Leptolucania ommata

10 Ellis Bay Pond, Baker County, Fla. (UF uncat.)

Empetrichthys latos

2 Nye County, Nevada (UMMZ 140490)

Crenichthys nevadae

2 Nye County, Nevada (UMMZ 132173)

Crenichthys baileyi

2 Lincoln County, Nevada (UMMZ 125006)

Profundulus hildebrandi

2 Chipas, Mexico (UMMZ 166691)

Aphanius cypris

1 Ak-Gol bei Ergli, Turkey (ZSZM uncat.)

Aphanius fasciatus

1 Kucukeekmece, Istanbul, Turkey (ZSZM uncat.)

Aphanius chantrei

1 Cihanbeyli, Turkey (ZSZM uncat.)

Aphaniops _dispar_

1 Aquarium Stock (ZSZM uncat.)

Anatolichthys _transgrediens_

1 Aci-Gol, Turkey (ZSZM uncat.)

Kosswigichthys _asquamatus_

1 Hazor-Golu, Turkey (ZSZM uncat.)

Valencia _hispanica_

1 Aquarium Stock (ZSZM uncat.)

Rivulus _bondi_

5 Caracas, Venezuela (UMMZ 141915)

Cynolebias _whitei_

1 Rio de Janeiro (USNM uncat.)

Austrofundulus _stagnalis_

4 Lagunillas, Venezuela (UMMZ 141919)

Aphyosemion _caeruleum_

2 Lagos, British Nigeria (ZSZM uncat.)

Nothobranchius _taeniopygus_

1 Kafue River, Zambezi River System (RU uncat.)

Aplocheilus _panchax_

4 Lake Pandjaloe, Java (UMMZ 146561)

Oryzias _latipes_

4 Pond beside Matsu Bay, Japan (UMMZ 146592)

Orestias _agassizii_

4 Rio Grande de Lipez, Bolivia (CAS 16125)

Micropanchax loati

1 Nile (BMNH 1907.12.2.2709-11)

Aplocheilichthys schoelleri

1 Nile (BMNH 1907.12.2.2649-50)

Aplocheilichthys johnstni

2 Chobe River, Upper Zambezi River System (RU uncat.)

Aplocheilichthys katangae

1 North Rhodesia (RU uncat.)

Lamprichthys tanganicanus

1 Lake Tanganica (ZSZM uncat.)

Methods

Due to the small size of the fishes included in the present study, it was impossible to prepare dry skeletons by maceration or by any other method. Therefore, the specimens were cleared, stained and placed in glycerine according to the method of Davis and Gore (1936) and Evans (1948). In order to see the details of the osteology, specimens were dissected free of tissue under the binocular microscope and, with the aid of a camera lucida, drawings were made at successive stages of dissection.

In order to determine which structures vary with age or between sexes, series of specimens were prepared of each sex and of graded sizes from juveniles to adults. This was possible only with the local species which were available in sufficiently large numbers; other species were represented by few specimens.

Before attempting an analysis of the osteological characters of the various genera of cyprinodonts, it seemed desirable to have a general idea of cyprinodont osteology. The skeleton of *Cyprinodon variegatus variegatus* (Lacepede) is therefore, described in detail. This species was selected to serve as a basis of comparison in an analysis of the comparative osteology of the various genera because of its widespread distribution and the abundance of material available for this study.

Two other species of Cyprinodon, *C. salinus* Miller and *C. macularius* Baird and Girard, have also been included in the general description in order to cover the range of osteological variation within the genus. Later in the study it was found that the monotypic genera *Floridichthys*, *Jordanella*, *Garmanella*, and *Cualac* agree sufficiently with *Cyprinodon* in osteological characters to permit them to be treated as a group in both the descriptive and the analytical phases of the study.

Additional to this group composed of *Cyprinodon* and its allies, other groups became apparent and have received group treatment similar in approach to that used in the first group. These groups are listed for reference purposes as follows:

Group I (cyprinodontids). *Cyprinodon*, *Floridichthys*, *Jordanella*, *Garmanella*, and *Cualac*.

Group II (aphanids). *Aphanius*, *Aphaniops*, *Anatolichthys*, and *Kosswigichthys*.

Group III (fundulids). *Fundulus*, *Lucania*, *Adinia*, *Chriopeops*, *Leptolucania*, *Empetrichthys*, *Crenichthys*, *Profundulus*, *Cubanichthys*, and *Oxyzygonectes*.

Group IV (valencids). *Valencia*.

Group V (aplocheilids). *Aplocheilus*, *Aphyosemion*, *Nothobranchius*, *Rivulus*, *Cynolebias*, *Austrofundulus*, *Epipletys*, *Pachypanchax*, *Rachovia*, *Pterolebias*, *Trigonectes*, *Rivulichthys*, *Neofundulus*, and *Hubbsichthys*.

Group VI (aplocheilichthyians). *Aplocheilichthys*, *Hypsopanchax*, *Platypanchax*, *Procatopus*, *Micropanchax*, *Cynopanchax*, *Plataplocheilus*, and *Lamprichthys*.

Group VII (oryzianes). *Oryzias*.

Group VIII (orestians). *Orestias*.

GROUP I

Composition, Range and Habitat

The geographic range of this group extends from the Colorado River system and the eastern and southern United States to the Caribbean coast of South America.

The following genera are included:

Cyprinodon Lacepede. About 13 species.

Range: eastern, southern and southwestern United States to northern South America and the West Indes (Andros Island, Bahamas; Etang Saumatre, Haiti and Jamaica).

Habitat: mostly in the quiet shallows of fresh, brackish and salt waters, including desert warm springs; not adapted as active swimmers and consequently seldom found in swift or turbulent waters.

Floridichthys Hubbs. Monotypic.

Range: Florida and Yucatan.

Habitat: chiefly marine littoral.

Jordanella Goode and Bean. Monotypic.

Range: endemic to Florida

Habitat: swamps, ponds and ditches.

Garmanella Hubbs. Monotypic.

Range: Yucatan Peninsula southward to Corozal, British Honduras.

Habitat: brackish to nearly fresh waters.

Cualac Miller. Monotypic

Range: known only from warm springs in San Luis Potosi, Mexico.

Osteology

The following species of Group I have been studied: Cyprinodon variegatus variegatus (Lacepede), C. macularius Baird and Girard, C. salinus Miller, Floridichthys carpio carpio (Gunther), Jordanella floridae Goode and Bean, Garmanella pulchra Hubbs, and Cualac tessellatus Miller.

The osteology of various genera has been considered under the following heads: head skeleton, vertebral column, and fins and fin-skeleton.

Cyprinodon v. variegatus was selected for detailed description and basis of comparison. With appropriate modifications the following account will apply not only to all the genera of Group I but also to all other Groups under consideration. Subsequent descriptions, therefore, consist mainly of a delineation of points of difference from the Cyprinodon pattern.

Head Skeleton (Figs. 1 and 2)

The head skeleton is composed of the skull proper and the visceral skeleton which includes the jaws, the hyoid, the branchial arches and the bones of the operculum. Elements of the head skeleton consist of the cartilage bones, the secondarily developed investing bones, and cartilaginous structures which remain unossified even in the adult.

In adult specimens of Cyprinodon v. variegatus the head is almost as long as deep. Its greatest depth is near the posterior end and from that point it tapers sharply toward the jaws. It is also broader posteriorly than in either the anterior or the midorbital regions (Figs. 3A and 3B). The narrowness of the interorbital region is due to weakly developed supraorbital processes which are slightly raised above the general level of the skull and consequently appear to be convex dorsally. The interorbital width in the middle of the orbital region is about half the width of the skull taken between the outer edges of the pterotics. The premaxillary processes are short and in prepared skeletons, there is a distinct gap between them and the maxillae.

Skull (Figs. 3 and 4)

The skull proper consists of that complex of bones and cartilages which are situated around the brain and cannot be readily separated from each other. This complex includes all the bony structures developed from the original chondrocranium as well as the secondary bones attached to it including the vomer and the parasphenoid.

The dorsal surface of the skull is almost flat except for the supraorbital processes of the frontals which are mildly convex. The posterolateral corners of the skull, on either side of the epiotics and the posterior portions of the frontals, are situated below the general level of the skull and thereby form a depression. The supraoccipital processes are slightly raised from the general level of the skull due to the presence of a small supraoccipital crest.

On the ventral side, the anterior half of the skull is occupied by the large orbits which are separated by a narrow parasphenoid in between. The portion of the skull represented by the parasphenoid appears to be a little elevated below, while small depressions occur in the posterolateral corners. Two small elevations are present, one on either side, around the area occupied by the large sacculiths. Most of the cartilage bones are separated from each other by thin pieces of cartilage in the interspaces between their margins.

The anterior region of the brain case is poorly provided with bony structures. There is a small ethmoid cartilage in front, but both the orbitosphenoids and the basisphenoid are absent. The alisphenoids are very small, posteriorly situated, and do not meet in the median line.

The skull, for the purpose of more detailed description, may be divided into four main regions: the ethmoidal, the orbitotemporal, the otic or auditory, and the occipital.

Ethmoid Region (Figs. 1 and 6)

The ethmoid region forms the most anterior portion of the cranium. The ethmoid cartilage extends from under the anterior margins of the frontals up to the maxillae. Dorsally the entire region is roofed over by the nasals and the anterior margins of the frontals; ventrally the mesethmoid, the vomer and the tip of the parasphenoid form the floor; and laterally the lateral ethmoids provide the sides.

Ethmoid cartilage (Fig. 6A). The ethmoid cartilage is a median bar-like structure which forms the anterior margin of the brain case and it has the mesethmoid lodged in its floor. The vomer lies ventral to the mesethmoid and extends anteriorly for a considerable distance to come in contact with the maxillae.

Mesethmoid (Figs. 6A, 6B). The mesethmoid is a heart-shaped, scale-like bone. It lies in the anterior concacity of the median ethmoid cartilage and is supported from below by the vomer. The broad base of the mesethmoid is directed anteriorly while its conical portion points backward.

Lateral ethmoid (Figs. 1 and 6). The lateral ethmoids are ossified, paired bones of the preorbital region where they lie along the outer sides of the ethmoid cartilage. They come in contact with the lachrymals and are covered dorsally by the anterior margins of the frontals and the posterior margins of the nasals. Each ethmoid is of very irregular shape and consists of an elongated anteroposteriorly directed medial part and a more or less vertically disposed transverse expanded plate. The anterior region of the medial part has an articulating facet for the ethmopalatine process of the autopalatine while its posterior portion has an articulating surface for the parasphenoid. The vertically disposed expanded plate forms the anterior boundary of the orbit and laterally comes in contact with the lachrymal. The olfactory nerve emerges from the foramen advehens in the lateral ethmoid to innervate the olfactory organ.

Nasals (Figs. 1, 2A and 6F). The nasals are a pair of elongated and somewhat triangular bones. They are situated immediately anterior to the frontals where they pass over the lateral ethmoids and come in contact with the upper portion of the maxillae. Ventrally, the nasals come in contact with the lateral ethmoids and the palatine heads; dorsally, their upper surfaces contain a tubular supraorbital sensory canal.

Vomer (Figs. 6D and 8). The vomer is a flat, T-shaped, membrane bone attached to the ventral surface of the ethmoid region of the skull. It lies in the median plane and its broad anterior portion extends forward a considerable distance and comes in contact with the upper portion of the maxillae. Its narrow posterior portion extends backward over the floor of the ethmoid region and is inserted in a groove of the parasphenoid. The vomer supports the mesetmoid on its upper surface and lacks teeth not only in Cyprinodon v. variegatus but also in all other Cyprinodonts examined during this study except for the aplocheilids (Group V).

Orbitotemporal region (Figs. 3A, 3B and 7)

The orbitotemporal region is imperfectly developed and it cannot be divided clearly into orbital and temporal or sphenoidal regions. The parietals, the basisphenoid and the orbitosphenoids are absent; the alisphenoid is small and confined to a corner between the sphenotic and orbital portions of the frontal. The brain case in this region lacks bony support to its lateral walls. The eye, which occupies the entire lateral orbital space, covers the brain case from the sides. The orbital space is bounded anteriorly by the lachrymal and the lateral ethmoid and posteriorly by the alisphenoid, sphenotic and the postorbital. However, the frontals are well developed and compensate for the scanty development of the other bones. They cover the entire orbitotemporal region and extend over the posterior part of the ethmoidal region. The ventral side of this region is supported entirely by the elongated and narrow parasphenoid. The orbitotemporal region, although forming a major portion of the skull, has only a small number of bones, viz., the paired frontals on the dorsal side, the bones of the circumorbital series and the alisphenoids on the lateral sides, and the parasphenoid on the ventral side. Except for the alisphenoids which are replacing bones, all the others are membrane bones.

Frontals (Figs. 3A, 7A, 7B). The frontals cover a considerable part of the skull on the dorsal side. They are broad, flat and elongated ossified plates with their median margins overlapping each other. Their posterior parts diverge laterally and a median supraoccipital bone is wedged between them. The anterior margins of the frontals overlap the ethmoid cartilage and portions of the lateral ethmoids. Posteriorly they extend over the supraoccipital and also come in contact with the otic bones laterally.

Owing to corresponding curvatures on its dorsal side and the disposition of the supraorbital channel, the dorsal surface of the frontal appears to be divided into three regions, the interorbital, supraorbital, and sphenoidal or temporal. Moreover, a distinct triradiate ridge on its ventral surface (visible from above in cleared and stained specimens) separates these regions clearly. Both the interorbital and the supraorbital areas are convex dorsally. The sphenoidal area is situated behind the interorbital and the supraorbital areas and in front of the supraoccipital bone and the otic regions. The alisphenoid bounds the sphenoidal region of the frontal anterolaterally. The supraorbital channel is perforated by the lateralis fibers which pierce the bone in order to inervate it.

Parasphenoid (Figs. 3B and 8). The parasphenoid is applied to the skull from the ventral side and forms a narrow floor for the brain case along almost its entire length. Anteriorly it is wedged between the mesethmoid above and the vomer below. Its anterior end is somewhat obtuse and broadened, and has a small depression into which the narrow posterior end of the vomer is inserted. Posteriorly, the parasphenoid extends over the mesial portions of the prootics and finally overlaps almost all of the ventral half of the basioccipital. At the anterior portion of the prootic, on each side, the parasphenoid sends off a lateral process which joins the lateral commissure. At about the same level from where the lateral processes are produced a pair of small V-shaped processes arise from the inner surface of the parasphenoid. These inner processes are short, point upwards and do not extend laterally. A prominent median ridge is present on the ventral surface of the parasphenoid in the interorbital region. The parasphenoid is hollow internally. A myodome, or the so-called eye muscle canal (Allis, 1919), is lacking. This lack of a myodome is due to the fact that the inner processes of the parasphenoid are short and do not extend laterally to join either the prootic or the alisphenoid.

Alisphenoid (Figs. 5B and 7D). The alisphenoids are situated in the posterior orbital region of the skull. Each alisphenoid is a small roughly triangular bone, wedged in between the frontal above and the sphenotic behind. It also comes in contact with the anterolateral extension of the prootic and its anterior portion is lodged in a depression on the inner side of the frontal.

Circumorbital series (Figs. 1 and 7A, 7B and 7C). There are only two bones in the circumorbital series, a lachrymal in the preorbital region and a postorbital in the posterior region of the orbit. There are no supra- or suborbitals. In place of the former the supraorbital process of the frontal protects the eye from above.

Lachrymal. The lachrymal is situated in the preorbital region of the skull. It is loosely embedded in the tissue between the maxilla in front and the lateral ethmoid behind, and is in contact with both of these bones. It is broad and roughly boat-shaped. Its outer surface is channeled for the sensory canal system.

Postorbital. The postorbital forms the posterior boundary of the orbit and is shaped like an elongated scoop. It lies external to the vertical limb of the sphenotic and is channeled for the sensory canal system. Its upper end rests in a small notch of the frontal, while its lower end reaches up to the upper portion of the preopercle.

Sclerotic bones. There are two broad, cup-shaped sclerotic bones in the sclerotic coat of each eye. These sclerotic elements are located in the anterior and posterior corners of the eye opposite the lachrymal and the postorbital bones respectively. They are stained red with alizarine dye just as are the other bony elements. This rather unusual occurrence of bony structures in the eye has also been noted by Ramaswami (1945) in *Gambusia affinis holbrooki* and by Kulkarni (1948) in *Aplocheilus lineatus*.

Otic region (Figs. 1, 3A, 3B, 8 and 9)

The otic region is composed of four bones: epiotic, prootic, pterotic and sphenotic. These are situated on either side in the posterolateral corners of the skull. The opisthotic is absent. A rather prominent unossified space is present between the epiotic, pterotic, sphenotic and the posterior edges of the frontal through which one of the otoliths, the sagitta, can be seen.

All of the otic bones are irregularly shaped because they from the walls of an irregularly shaped otic capsule. Internally, the inner laminae of these bones are ossified in such a manner so as to form canals or tunnel-like passages for the accommodation of the semicircular canals of the membranous labyrinth. Similarly, recesses are developed on the inner surfaces of the otic bones for ampullae and otoliths.

Prootic (Figs. 3B and 8). The prootic is situated anterior to the basiooccipital and exoccipital, and mesially to the pterotic, sphenotic and alisphenoid. It is flattened towards its outer surface while internally it is provided with two or three small ridges radiating laterally from its center. The anterolateral ridge is the most prominent of all and comes in contact with the alisphenoid and sphenotic.

The other ridges are smaller and radiate laterally from the base of the larger ridge, enclosing between them a depression on the inner side of this bone. This depression, along with similar depressions in the basioccipital and exoccipitals, provide a recess for the sagitta and the ampullae of the posterior and the anterior semicircular canals. Another small depression is located more anteriorly and immediately behind the trigemino-facialis chamber. The prootic invades the lateral commissure and sends a small process anterodorsally. This process is perforated by the three orifices for the exit of the lateral line branches. The lateral commissure is joined by the posterolateral limb of the parasphenoid which extends laterally towards it. Another small process from the ventral limb of the parasphenoid joins the anterodorsal extension of the prootic. The anterior opening of the trigemino-facialis chamber lies between the small process from the ventral limb of the parasphenoid, anterodorsal extension of the prootic, and the ossified lateral commissure. The inner limb of the parasphenoid is small and does not extend laterally to join the anterodorsal extension of the prootic. Additional to the three orifices already described, there are two more openings on the prootic, one just under the origin of the ventral limb of the parasphenoid, and the other mesial to the posterior opening of the trigemino-facialis chamber. The first one is the orifice for the arteria carotis interna while the second accommodates the orbital artery. The posterior myodome from which the posterior rectus muscle of the eye emerges is not evident. Instead, the posterior rectus muscle emerges from a wide recess above the prootic and the parasphenoid.

Sphenotic (Figs. 1, 2A and 9C). The sphenotic occupies the anterolateral border of the otic capsule. On its ventral surface there is a depression for the anterior condylar head of the hyomandibular. The sphenotic is produced into an elongated limb which runs downward in the postorbital region. Externally, the postorbital covers the downwardly projecting limb of the sphenotic. Anteriorly, the sphenotic comes in contact with the alisphenoid, dorsally with the frontal, posteriorly with the pterotic, and mesially with the prootic. Internally the sphenotic is excavated into a short tunnel for the anterior semicircular canal. Along with the pterotic and the prootic, the sphenotic forms a recess for the ampulla between the anterior and the horizontal semicircular canal. Posterolaterally the sphenotic is produced into a blade-like expansion which meets a similar anteriorly directed expansion of the pterotic.

Epiotic (Figs. 1, 2A, 4B and 9B). The epiotic occupies the posterodorsal border of the otic capsule and comes in contact, anteriorly with the frontal and the supraoccipital, laterally with the pterotic, and posteriorly with the exoccipital. It covers the posterior semicircular canal and, together with the exoccipital, forms a recess for the ampullae of the posterior and horizontal semicircular canals of the membranous labyrinth. Posterolaterally a limb of the forked posttemporal is firmly attached to the epiotic.

Pterotic (Figs. 1, 2A, 4B and 9A). The pterotic occupies the posterolateral border of the otic capsule and lies at a conspicuously lower level than the adjacent bones. The depression formed by this unusual position is filled with muscle fibres. The pterotic forms the lateral margins of the skull and extends both dorsally and ventrally. Mesially it is in contact with the epiotic, ventrally with the prootic and anterolaterally with the sphenotic. It is tunneled internally for the horizontal semicircular canal and has a prominent, ventrally disposed facet for the articulation of the posterior head of the hyomandibular.

Otoliths (Fig. 9D). The sagitta (sacculith) is the largest otolith. It lies vertically in a recess formed by the prootic, basioccipital and the exoccipital. It is high and roughly circular. Its mesial border is slightly convex while its outer surface is slightly concave. Its dorsal rim is shorter than the ventral edge and is provided with four to five indentations. Almost in the middle of its mesial convex side, a wide and straight sulcus opens toward the anterior rim. The posterior end of the sulcus is rounded and does not quite reach the posterior rim. Such a sagitta has been termed as the "Microcyprinid" type by Frost (1926). The jugular foramen is located immediately behind the sagitta.

The asteriscus (lagenalith) is well developed. It is about half the height of the sagitta and lies upright in a recess of the exoccipital.

The lapillus (utriculth) is the smallest otolith. It is approximately bean-shaped and lies anterior to the sagitta in a recess of the prootic.

Occipital region (Figs. 1, 2A, 4 and 10)

The occipital region is formed by the union of four replacing bones, the supraoccipital, basioccipital, and the two exoccipitals situated on the dorsal, ventral and lateral sides of the skull respectively. The foramen magnum is formed collectively by two lateral exoccipitals, a ventral basioccipital and a dorsal supraoccipital. The occipital region is in contact with the otic region laterally, with the frontals dorsally and with the parasphenoid ventrally. The basisphenoid and the parietals are absent.

The occipital region is in intimate union with the first vertebra and articulates with it by an occipital condyle borne on the basioccipital and also by two rather poorly defined surfaces on the exoccipitals. This union is strengthened by the neural arches of the first vertebra which are separate and do not fuse dorsally into a neural spine. Instead they are applied on either side to the posterior edges of the supraoccipital and the exoccipitals. In adult specimens the fusion is so complete through secondary ossification around the area of contact that it is almost impossible to separate the first vertebra from the occipital region without damage to the parts. Due to this disposition of the first vertebra there is a considerable gap between it and the second vertebra (Fig. 5). Other modifications of the first vertebra are described later in connection with the account dealing with the vertebral column.

Supraoccipital (Figs. 3A, and 11B). The supraoccipital is unusually large and constitutes a prominent element in the posterior region of the skull. Anteriorly it extends beneath the frontals, dorsolaterally it comes in contact with epiotics, and ventrolaterally it meets the exoccipitals. The supraoccipital contributes to the formation of the foramen magnum, and forms a prominent dome-shaped structure over it. Being membrane bones, the frontals are applied secondarily to the cranium and consequently overlap the margins of the supraoccipital on either side and thereby reduce the exposed surface of the latter considerably. From its posterodorsal surface, two supraoccipital processes extend posteriorly and slightly upward from the general level of the skull and are thus situated above the small supraoccipital crest. These processes are in the form of a pair of vertical laminae, separate throughout in young specimens, but in adults they become fused proximally due to additional ossification. In the anteromedian portion of the supraoccipital, there is a cartilaginous area which is lightly colored in all stained specimens. The area has a thin sheet of cartilage on its inner side which divides into a pair of narrow bands. These bands proceed forward on each side to meet the alisphenoid.

Exoccipitals (Figs. 4, 10A, 10B and 11A). The exoccipitals are paired bones and are situated in the posterior occipital region. They, rather than the opisthotics which are absent, take part in the formation of the otic capsule. Thus each exoccipital becomes the auto-occipital but the term exoccipital is retained here for convenience (Kulkarni, 1948). The exoccipitals form the sides of the foramen magnum and are separated from each other dorsally by the dome-shaped supraoccipital which completes the foramen from above. Each exoccipital bears a poorly defined articulating surface around the ventrolateral corner of the foramen magnum. These surfaces can only be seen in young specimens after carefully removing the first vertebra which is in intimate contact with the occipital region through its neural arches. In adult specimens, however, the neural arches and the posterior extremities of the supraoccipital and the exoccipitals are co-ossified and it is impossible to separate the first vertebra from the skull without damaging some of the adjacent parts. Laterally the exoccipital comes in contact with the pterotic, dorsally with the supraoccipital, and dorsolaterally with the epiotic. From the foramen magnum, the exoccipital extends laterally as well as ventrally to join the pterotic and the basioccipital respectively. Along with the pterotic and the basioccipital, the exoccipital encloses a large recess for the ampulla and two otoliths, the sagitta, and the asteriscus. Being produced in different directions the bone is irregular in shape. Internally each exoccipital sends a vertical support or plate to the inner side of the basioccipital (Fig. 10B). Kulkarni (1948: 75) reported a similar arrangement in Aplocheilus lineatus but was doubtful of its origin.

Two large and one small foramina are situated on the anteroventral aspect of the exoccipital and occur together in the same depression. The jugular foramen (Fig. 3B) is large and occurs immediately behind the recess for the sagitta. The lower limb of the forked posttemporal is attached to the exoccipital through a small cup-like bone just behind the jugular foramen. The hypoglossal foramen is located on the posterolateral aspect of the exoccipital, above the poorly defined articular surface for the first vertebra.

Basioccipital (Figs. 4A, 10 and 11A). The basioccipital forms the floor of the foramen magnum. It is an elongated bone, narrow posteriorly and broad at the anterior extremity. Anteriorly it is in contact with the mesial portions of the prootics while laterally it joins the exoccipitals. The posterior extremity of the parasphenoid is applied to its anterior end. Internally the anterolateral corners of the basioccipital are excavated and form a part of the recess for the sagitta. Posteriorly the bone has a large circular condyle for articulation with the centrum of the first vertebra (Fig. 11A). The ventral, outer surface of the basioccipital is flat but internally the two bony plates descending down from the exoccipitals cut the bone into a median portion and two lateral corners. Into the median portion is lodged the posterior part of the medulla oblongata. The plates thus separate the brain case from the auditory capsules and also strengthen the occipital region internally. A foramen is present on either side of the basioccipital at almost on the same level as the jugular foramen on the exoccipital.

Visceral skeleton

The visceral skeleton consists of seven arches which may be divided into three constituent groups: (1) the mandibular arch forming the suspensorium of the jaws, (2) the hyoid arch forming the hyoid cornu, and (3) the branchial arches. The first two arches are more specialized than the others and are closely associated with the chondrocranium. The first, or mandibular arch, gives rise to palatoquadrate and mandibular bars which support the upper and lower jaws respectively. The second, or hyoid arch, gives rise to the hyomandibular which provides attachment for both the palatoquadrate and the hyoid arch. The next four arches support the gill filaments and the seventh is reduced to the tooth-bearing inferior pharyngeal bones.

Mandibular arch (Figs. 1, 12 and 13)

The palatoquadrate bar of the mandibular arch shows two independent ossifications, the autopalatine and the quadrate. A thin mesopterygoid is attached to the above two bones from behind. The metapterygoid is absent. Meckel's cartilage, which forms the lower jaw during the embryonic condition, becomes ossified into the articular except for a portion of the original cartilage which persists in the adult. The tooth-bearing dentary grows around the distal part of Meckel's cartilage and forms the biting part of the lower jaw. A small angular and the sesamoid articular are also located on the inner portion of the jaw. The upper jaw is formed of two pairs of dermal bones, the premaxillae and the maxillae.

Quadrate (Figs. 1 and 12). The quadrate is a large bone situated anterior to the mesopterygoid, the symplectic, the opercle, and the interopercle bones. It consists of two portions, a posteriorly directed lower limb and a thin membranous vertical portion. The lower limb of the quadrate lies over the preopercle, the interopercle and the symplectic while the vertical portion of this bone extends upward and joins the autopalatine and the mesopterygoid. The quadrate bears a prominent, pully-like condylar head for articulation with the articular and thus helps to connect the upper and the lower jaws.

Palatine. The palatine, or autopalatine, is the most anterior bone of the palatoquadrate bar. Its lower, membranous part is applied to the vertical portion of the quadrate while the upper, thicker portion extends dorsally to come in contact with the ethmoid and the maxilla through its two heads, the ethmopalatine and the restropalatine, respectively.

Dentary. The dentaries form the anterior portion of the two rami of the lower jaw and they come in contact with one another anteriorly through a ligament. They are, however, not fused to form a mandibular (mentomeckelian) symphysis. Together, the dentaries form the entire tooth bearing part of the lower jaw. The posterior part of the dentary is excavated to receive the distal portion of the articular bone.

Articular. The articular forms the ventrolateral margin of the lower jaw. It is dagger-shaped, with its stem and blade of unequal length. The anteriorly directed blade of this bone, along with Meckele's cartilage, is lodged into the excavation of each dentary as mentioned previously. The vertically directed portion of the stem is expanded and prominent, while the ventrally directed piece is small. The sesamoid articular lies on the inner side of the articular near the proximal portion of the elongated blade. On its posterior end the articular bears a prominent articular facet for the condylar head of the quadrate.

Angular. The angular is a very small and irregular piece of bone attached to the ventral portion of the articular and positioned closed to the articular facet.

Premaxillae. The premaxillae are prominent tooth-bearing bones which, together, form the entire upper jaw. The premaxillae of the two sides meet anteriorly in the midline but do not form a fused symphysis. Each premaxilla consists of a horizontal tooth-bearing portion bordering the mouth and an edentulous arm which extends backward and downward to terminate in a spine. This arm is slender at the angle of the mouth but flattens posteriorly before finally terminating in a spine. The spine lies internally to the distal, pointed portion of the maxilla and projects backward beyond the latter. The horizontal tooth-bearing portions of the premaxillae are produced into small, triangular premaxillary processes which extend backward. The two processes run close together without actually touching each other mesially and the extremities of these processes diverge slightly from each other. The entire premaxilla presents the appearance of an "S" with the extremities slightly pulled apart. There is a close resemblance, in both number and shape, between the teeth of the premaxillary and the dentary.

Maxillae. The maxillae are edentulous and being situated behind the upper jaw, they do not take part in its formation. Each maxilla is a straight rod-like bone. Its lower end lies external to the terminal spine of the premaxilla and then ascends upward toward the nasal bone. On reaching the nasal each maxilla sends off a dorsally expanded outer process. Another but slenderer process is mesially situated and proceeds forward. The nasal bone comes in contact with the dorsally expanded process of the maxilla, whereas the lachrymal comes in contact with the straight rod-like portion of the maxilla at its middle. Each maxilla bears toward its posterior upper surface a facet for the rostropalatine head of the autopalatine and each is also in contact with the lateral extremity of the vomer.

Teeth (Figs. 1, 2, 12 and 13). Both the premaxilla and the dentary bear a single row of moderately stout tricuspid teeth. Each tooth is provided with two laterally pointed cusps and a blunt median cusp.

Hyoid arch (Figs. 1, 12, 13 and 14)

The second, or hyoid, arch gives rise to the hyomandibular, the symplectic and the hyoid cornu. The hyomandibular provides attachment for the jaws, the hyoid cornu and the opercular bones. The palatoquadrate bar is suspended from the skull through the hyomandibular and therefore the suspensorium is hyostylic.

Hyomandibular. The hyomandibular is an elongated, roughly quadrilateral bone, located vertically in the postorbital region of the skull. It has two prominent condylar heads (Fig. 12) at its upper extremity by which it is articulated with the sphenotic and the pterotic bones. These two latter bones have corresponding facets for the heads of the hyomandibular toward their lower surfaces. Another articulating head is situated toward the posterior surface of the hyomandibular through which it provides attachment to the operculum. Below the two condylar heads, two prominent ridges proceed downward. These ultimately join and then expand into a wing-like projection. The preoperculum is adnate to the posterior extremity of this wing-like structure. The lower portion of the hyomandibular is flattened into an elongated rod-like structure and ends in a truncated facet. At the lower extremity of the hyomandibular a small cartilaginous area provides attachment to the truncated upper extremity of the symplectic and a small interhyal (Fig. 12). The foramen for the ramus hyomandibularis nerve is located in the middle of the hyomandibular.

Symplectic. The symplectic is a plough-shaped bone, lying below the hyomandibular. It consists of an upper rod-like portion and a wing-like lower membranous expansion. The anterior apex of the symplectic is firmly wedged in a mesial notch of the posteriorly directed lower limb of the quadrate.

Hyoid cornu (Fig. 14). The hyoid cornu or hyobranchial skeleton, consists of a pair of arches, one member of which is situated on either side of the buccal cavity. Each arch originates from a cartilaginous piece at the lower extremity of the hyomandibular of its side, and proceeds downward and forward to meet the corresponding arch from the other side in the midventral line on the floor of the buccal cavity. Each arch is made up of four segments, the interhyal, the epihyal, the ceratohyal and the hypohyal. The hypohyals of the two sides are very close together in the median line and, on their upper surfaces, support a median triangular basihyal. The basihyal forms the anteriormost, median part of the hyoid cornu and supports the tongue. On their ventral aspects, the two hypohyals come in close approximation with another median piece, the urohyal. The hypohyals, the basihyal and the urohyal, although lying close together, remain separate and are joined with each other only by muscles and ligaments.

Interhyal (Fig. 1). The interhyal, or stylohyal, forms the dorsal segment of each of the two arches. It is a small hourglass-shaped bone, disposed vertically toward the mesial side of the upper margin of the membranous portion of the preopercle where it is attached to a small cartilaginous element lying below the rod-like extremity of the hyomandibular. It provides attachment to the next piece of the arch, the epihyal, by means of a cartilaginous element. Goodrich (1958) considered the interhyal as probably a new formation rather than as an epibranchial with which it has been compared by others.

Epihyal. The epihyal proceeds anteroventrally from the interhyal to which it is attached by an articulating facet on its dorsal extremity. It is a triangular piece with its base directed forward and the apex hanging down from the interhyal. It is in touch with the following segment, the ceratohyal, by way of a cartilaginous interspace between them. The dorsal sides of these two bones, however, are devoid of any cartilaginous interspace. Due to a secondary thickening of the bones, a ridge is formed along the entire dorsal edges of the epihyal and the ceratohyal. The most posterior branchiostegal ray is attached on the outer side of the epihyal by a flattened articulating surface of the ray.

Ceratohyal. The ceratohyal follows immediately from the epihyal with which it is connected along its dorsal edge through the ridge mentioned previously. It has a broad base, but its anterior end becomes narrow where it is provided with an inner and slightly raised articulating facet and an outer almost rectangular cavity. The ceratohyal joins the hypohyal of its side through the two facets mentioned above. Three branchiostegals are attached to the ceratohyal toward its outer side.

Hypohyal. The hypohyal is in close contact with the ceratohyal. The hypohyals of the two sides come very close together in the median line but their mesial sides do not fuse and the space between the two is filled by a small cartilaginous area.

Urohyal, Branchiostegals and Opercular Bones

The urohyal, the branchiostegal rays and the opercular bones, although not belonging to the hyoid cornu, are described here in view of their close association with the latter.

Urohyal. The urohyal, or basibranchiostegal, is a thin vertically disposed plate situated very close to the posteroventral portions of the hypohyals and in the middle of the angle formed by the meeting of the two arches of the hyoid cornu. The urohyal is is approximately triangular in shape with its apex near the angle of the hyoid cornu and the remainder of its body lying behind. The apex of the urohyal is provided with two short processes from which two ligaments proceed forward to attach to the ventral surfaces of the hypohyals. A third, but smaller, process from the apex of the urohyal is directed upward and comes in contact with the first basibranchial.

Branchiostegals (Fig. 14). In *Cyprinodon v. variegatus*, *C. macularius* and *C. salinus* there are six branchiostegal rays on each of the two arches of the hyoid cornu. These six rays are arranged in two groups according to their structure and manner of attachment to the hyoid cornu. The first group contains two branchiostegals which are comparatively small and close together but, as a group they are separated by a considerable gap from the four rays of the second group. The two rays of the first group are attached in a conspicuous groove on the inner aspect of the ceratohyal and are more firmly attached to the hyoid arch. These two rays are of a uniform rounded shape except toward the posterior extremities where they become pointed.

The four branchiostegals of the second group are sabre-shaped, the two outermost more so than the others. All four rays of the second group are attached to the outer side of the hyoid arch, the three inner ones on the ceratohyal, and the outer one on the epihyal. The rays of the second group are flattened toward their proximal extremities where they join the hyoid arch and become narrower toward their free distal extremities; also they are broadest just behind their points of attachment to the hyoid arch. The outermost ray in the broadest and the longest, reaching up to the posterior extremity of the opercle. All the branchiostegal rays are folded below the opercular bones.

The number and the manner of attachment of the branchiostegals shows little variation. Out of twenty-three specimens of Cyprinodon v. variegatus examined, only one specimen showed a difference and it had three, rather than the usual two branchiostegals in the first group.

Floridichthys c. carpio, Jordanella floridae, Garmanella pulchra and Cualac tessellatus differ from this description in that they have only five branchiostegals, because the first group contains only one ray.

Considerable importance has been attached to the form and the arrangement of brachiostegals in different groups of fishes. Hubbs (1919: 61) pointed out that in the higher groups of the teleosts there is " . . . a peculiarly constant arrangement of the branchiostegals." Again, while commenting upon the relationships of the order Cyprinodontiformes Hubbs (1924: 7) stated: "Finally a fact perhaps more conclusively indicative of a more advanced organization, the branchiostegal rays of the Cyprinodontes are of the acanthopterygian type, whereas those of the Haplomi are of a distinctly more generalized type." The arrangement of the branchiostegals of the cyprinodonts in the present study agrees with the description given by Hubbs (1919), and thus justifies for tham a place near the Acanthopterygii as was pointed out by Hubbs (1919, 1924).

Opercular bones (Figs. 1, 12 and 13). The opercle is a prominent bone on the posterolateral side of the skull. Its upper, posterior, and lower edges are rounded while the anterior margin is straight. There is a rounded process on its anterior upper surface which extends beyond the articulating facet, the latter being present toward its inner aspect. The outer surface of the opercle is convex while its inner surface is concave. A concave articulating facet is present on the inner aspect of the opercle, by which it articulates with a corresponding convexity on the hyomandibular.

The preopercle lies immediately anterior to the opercle. Its posterior, vertically disposed arm comes in contact with the anterior margin of the opercle, while its lower limb is directed anteriorly to lie under the posteriorly directed lower limb of the quadrate. In between the two arms of the preopercle there is a thin membranous bony lamina which lies under the lower extremity of the hyomandibular and the posterior portion of the symplectic. The vertical and the lower arms of the preopercle are channeled for the lateral line sensory canal system. The preopercle overlaps the subopercle and the interopercle bones.

The subopercle lies below the opercle and is the innermost bone of the opercular series. It is somewhat triangular in shape with its base considerably broadened. Its upper spine-like apex lies below the preopercle. A prominent ridge is present on the spine and posterior to it there is a notch for the reception of the narrow lower portion of the opercle. The subopercle is overlapped anteriorly by the interopercle.

The interopercle is also triangular. Its apex lies under the posteriorly directed limb of the quadrate, its broad base overlaps the subopercle, while it is itself overlapped by the preopercle.

Branchial arches (Fig. 15)

The branchial skeleton consists of five branchial arches which are serially arranged immediately behind the hyoid cornu. Of these, the anterior four bear gills on their ventral surfaces but the fifth one is greatly modified to form the lower pharyngeal bones. Each arch is made up of two lateral halves which unite in the midventral as well as in the middorsal lines. Normally, each half of the arch is made up of a pharyngobranchial and an epibranchial on the dorsal side, a ceratobranchial on the lateral side, and a small hypobranchial near the midventral line. In addition to these, a single, median basibranchial is situated in the midventral line with which the two hypobranchial of the two sides are joined.

The branchial arches are variously modified to serve different functions in different regions of the pharynx. However, the corresponding segments of different arches show similar modifications and therefore, the corresponding segments from different arches are treated together in the description which follows.

Pharyngobranchials. The pharyngobranchials, or dorsal pharyngeal bones, form the dorsal segments of the branchial arches. They are flattened and moderately thickened structures provided with teeth. The pharyngobranchials of each side are in close contact and meet similar bones from the other side in the middorsal line.

There is a small but definite amount of muscle tissue between the pharyngobranchials of the two sides and, consequently, the bones are not fused together. These bones are provided with ventrally directed teeth which work against similar but dorsally directed teeth on the lower pharyngeals and help in mastication.

The first pharyngobranchial is a small cartilaginous piece attached to the first epibranchial and, unlike the other pharyngobranchials, it is not provided with teeth. The second pharyngobranchial is in close contact with the third and fourth pharyngobranchials, which are fused into a comparatively large plate. The second pharyngobranchial bears two rows of teeth and the fused plate usually has five rows. These teeth are relatively uniform in size except on the fused plate where there is medial area of larger teeth and a tendency for the teeth to become smaller toward the posterolateral corners of the plate. The arrangement of the teeth on these dorsal pharyngeal bones is such that the larger teeth occlude the smaller teeth on the lower pharyngeal bone, while the smaller ones occlude the larger ones. The teeth on the lower pharyngeals are typically compressed with lateral shoulders surmounted by hooks.

The description of the pharyngobranchials as given for *Cyprinodon v. variegatus* is applicable to *Jordanella floridae* and, in general, to the other species of Group I which have been examined. However, in *Floridichtys c. carpio* the first pharyngobranchial is distinct and is provided with about two rows of teeth (Fig. 15B); in *Garmanella pulchra* and *Cualac tessellatus* the fused third and fourth pharyngobranchials are thickened and bear about seven rows of teeth.

Epibranchials. There are four epibranchials, and these are connected with the pharyngobranchials and the ceratobranchials. The first two epibranchials are rod-shaped. The base of the first one by which it articulates with the ceratobranchial is broad. The third epibranchial is Y-shaped with one of its arms slightly shorter than the other. The fourth epibranchial is the most prominent of all. It is hammer-shaped and has a prominent head by which it articulates with the fused pharyngeal plate. It also has a prominent tuberosity for muscle attachment and it comes in contact with the fourth ceratobranchial by a pointed end.

Ceratobranchials. There are four ceratobranchials and these form the greater part of the branchial skeleton. Each ceratobranchial is an elongated and slightly arched structure and dorsolaterally each is joined to an epibranchial at the lateral margin of the pharynx. From this attachment with the epibranchials, the ceratobranchials bend sharply inward and converge mesially, ventrally, and anteriorly for some distance before meeting the corresponding hypobranchials. The first three ceratobranchials are alike in having attachment with the three separate hypobranchials. The fourth ceratobranchial is different in that it does not come in contact with the separate hypobranchial because, in all the species examined in the present study, the separate fourth hypobranchials are absent. Instead, the fourth ceratobranchials are joined directly to the cartilaginous tips of the second basibranchial. In this connection Ramaswami (1945: 38) observed that in both embryonic and adult Gambusia affinis holbrooki "The cerato- and hypobranchials of the fourth arch (hcp4.) are not demarcated, for a dentigerous inferior pharyngeal plate has come in contact with it." Similarly Kulkarni (1948) described the fourth ceratobranchial and the hypobranchials as being fused structures in Aplocheilus lineatus.

Gill-rakers are present on both the anterior and the posterior surfaces of the first four gill arches but the fifth arch, which is reduced to the lower phryngeal bones, has these structures only on its anterior surface.

Hypobranchials. The hypobranchials are associated only with the first three ceratobranchials and are situated on either side of the median line. Toward their outer surfaces they are in contact with the ceratobranchials by cartilaginous interspaces while mesially they are joined to the basibranchials.

There is no separate hypobranchial segment in the fourth arch. As mentioned above, Ramaswami (1945) and Kulkarni (1948) expressed the opinion that the inner end of the fourth ceratobranchial represents a fused structure formed by the union of a hypobranchial with the ceratobranchial. Chapmen (1934) arrived at a similar conclusion in respect to Novumbra, in which this structure also is absent.

Basibranchials. There are only two ossified basibranchials supporting each of the four branchial arches. These correspond to the second and third basibranchials of other fishes. However, there are two cartilaginous pieces both at front of the 'first' and 'second' basibranchials and these pieces may represent the unossified first and fourth basibranchials respectively.

Fifth arch, or lower pharyngeal bones (Fig. 16). The fifth arch forms the most posterior element of the branchial skeleton. Unlike a typical arch, the fifth branchial arch is modified into two pharyngeal bones which form the floor of the posterior region of the pharynx. The outer ends of these two bones taper and diverge from each other, but their anterior ends and mesial surfaces are straight and lie close together in the midventral line. Their anterior extremities approach the fourth ceratobranchials and are attached to the cartilaginous piece at the lower end of the second basibranchial. Teeth, similar in structure to those of the upper pharyngeal bones, are arranged in about five rows. Cualac and Garmanella differ from Cyprinodon in having about five rows of teeth. In all these forms, however, the teeth project into the throat and occlude similar teeth on the upper pharyngeals. On the ventral side of each pharyngeal bone there is a prominent ridge for muscle attachment.

Posttemporal (Figs. 1 and 22). The pectoral arch on each side is suspended from the skull by way of a forked posttemporal. Each posttemporal is a Y-shaped bone with the two limbs of unequal length forming the fork attached to a comparatively thick but short stem. The stem is applied to the supracleithrum, the upper and longer limb of the fork is applied to the epiotic; while the smaller and lower limb is attached by a small cup-shaped piece of bone to the exoccipital, at a point immediately posterolateral to the jugular foramen. The extremity of the limb applied to the epiotic is somewhat flattened and there is a prominent ridge for muscle attachment running on the outer and upper portion of the posttemporal.

Vertebral Column (Fig. 17)

The vertebral column may be divided into two parts, the precaudal, or trunk region, and the caudal region. The vertebrae are amphicoelous and show modifications in different parts of the vertebral column. These modifications are especially pronounced at the anterior end where the vertebrae come in contact with the skull, and at the posterior end where they contribute to the formation of the caudal fin skeleton.

Vertebral counts for three species of *Cyprinodon* and four related genera of Group I are given in Table 1.

TABLE 1

VERTEBRAL COUNTS FOR SEVEN SPECIES OF GROUP I CYPRINODONTS

Species and Number of Specimens Examined	Number of Vertebrae					
	23	24	25	26	27	28
Cyprinodon v. variegatus (23)				7	11	5
C. salinus (2)				2		
C. macularius (2)				2		
Floridichthys c. carpio (18)		18				
Jordanella floridae (23)			2	21		
Garmanella pulchra (5)		5				
Cualac tessellatus (5)					1	4

These five genera (Cyprinodon, Jordanella, Floridichthys, Garmanella and Cualac) agree in all essentials of their vertebral colmuns except for variation in number of vertebrae. Consequently, a description of the vertebral elements of Cyprinodon will suffice for all five.

Precaudal or trunk vertebrae (Fig. 17A)

There are 11 or 12 precaudal vertebrae and they differ most markedly from the succeeding caudal vertebrae in lacking haemal canals on the ventral surfaces of their centra. The first vertebra shows the greatest modification and has become closely associated with the occipital region of the skull. The second and third vertebrae have broader neural spines for muscle attachment than do the others. The following few (4 to 5) vertebrae still possess comparatively broad neural spines but these gradually become narrower posteriorly. The remaining trunk vertebrae assume more normal shapes except that in them the transverse processes are prominent and ventrolaterally located.

The first vertebra (Figs. 1, 5 and 18)

The first vertebra is in close contact with the occipital region of the skull. Its elongated, somewhat flattened, and membranous neural arches are applied to both the exoccipitals and the supraoccipital on either side of the foramen magnum. In complete skeletons, there is a distinct gap between the first vertebra and the second vertebra which follows it. Because the neural arches of the first vertebra fail to meet above, a true neural spine is lacking. The first vertebra also lacks transverse processes, and vertebral ribs. The epipleurals, which in the following vertebrae join the proximal parts of the ribs, are attached near the base of the neural arches of the first vertebra.

The second and third vertebrae (Fig. 1 and 5).

These vertebrae have very prominent laterally compressed neural spines which provide large surfaces for the attachment of the dorsal musculature. The transverse processes are short, cup-shaped, and intimately joined to the ventrolateral aspects of the neural arches. They are provided with ribs which like the rest of the trunk vertebrae, fit into the concavities of the transverse processes through the intervention of cartilaginous tips. Apertures for the exit of nerves are located immediately behind the transverse processes in the neural arches.

The remaining trunk vertebrae are much alike. In them the neural spines progressively become narrower, smaller, and more pointed; the transverse processes, although joined to the lateral aspects of the neural arches, become progressively more prominent and shift gradually to a more ventrolateral position on the centrum; and in one or two trunk vertebrae immediately preceding the caudals, the transverse processes point downward.

The caudal vertebrae (Figs. 17A, 17B and 17C)

The caudal vertebrae are characterized by the presence of haemal canals between the joined haemal arches. Occasionally the first caudal vertebra has a small haemal spine, but the following caudals possess elongated haemal spines. However, the neural and haemal spines of the caudal vertebrae which contribute to the caudal fin skeleton are more elongated and compressed distally.

These more posterior caudal vertebrae also possess membranous bony expansions of variable extent on the anterior extremities of their neural and haemal spines. The urostyle is conical in shape and has become completely consolidated with the fan-shaped median hypural. The blunt anterior end of the urostyle can be clearly seen at the base of the median hypural. There are two hypurals. The larger median hypural is fan-shaped and completely consolidated with the urostyle as mentioned above. The smaller hypural is entirely ventral in position and its shape, size, and position varies considerably. In large individuals there is a thin bony expansion on the anterior surface of the ventral hypural. In some instances the base of the ventral hypural is close to the urostyle while in others there is a considerable space between them. In one specimen of <u>Cyprinodon variegatus</u> the base of the ventral hypural is fused with the ventral side of the median hypural, toward the anterior end of the latter. There is one epural and it is similar in shape to the ventral hypural. These two bones flank the ventral and dorsal surfaces of the median fan-shaped hypural respectively.

Caudal Fin (Fig. 17C)

The caudal fin skeleton consists of the four terminal caudal vertebral segments, their flattened neural and haemal spines, one epural and two hypurals.

The neural and haemal spines of the last caudal vertebra, excluding the urostylar segment, are flattened and extend posteriorly to enter into the caudal fin skeleton. The dorsal hypural is fan-shaped and, along with the second hypural below and an epural above it, supports most of the caudal fin rays. The fin rays extend anteriorly over the neural and haemal spines of the last four caudal vertebrae. The number of the caudal fin rays varies from 27 to 31. All of the caudal fin rays are bifid at their bases; they are jointed and branched, except for a few small anterior caudal fin rays which are unbranched.

Dorsal Fin (Fig. 19)

The origin of the dorsal fin in these five genera of cyprinodonts is located well in advance of the anal fin. There are thirteen proximal radials or pterygiophores (interneurals) between the neural spines of the vertebrae. The first proximal radial differs from the others in that it does not have a fin ray to support, and it lacks both the distal as well as the median radials. This proximal radial may correspond to a keel-like structure noticed in many fishes, such as those described by Phillips (1942) for Sardinops caerulea and Witzman (1954) for Carnegiella vesca. The remaining twelve proximal pterygiophores have both distal as well as median pterygiophores associated with them and also support fin rays or lepidotrichia. The distal pterygiophores lie between the right and the left half of the bifid fin rays. Each distal radial is almost split into two by a median fissure. The median pterygiophores are located between the upper extremities of the proximal pterygiophores except between the first and second, where the median radial is absent.

Fin ray counts for Cyprinodon v. variegatus and four other related genera of Group I are given in Table 2.

TABLE 2

DORSAL FIN RAY COUNTS IN FIVE SPECIES OF GROUP I CYPRINODONTS

Species and Number of Specimens Examined	Number of Dorsal Rays							
	12	13	14	15	16	17	18	19
Cyprinodon v. variegatus (23)	15	8						
Floridichthys c. carpio (18)	10	8						
Jordanella floridae (18)					3	8	6	1
Garmanella pulchra (5)					3	2		
Cualac tessellatus (4)	1	3						

The first fin ray of the dorsal fin in Jordanella floridae is spinous and unsegmented throughout in contrast to the other four genera where all the fin rays are soft and segmented. In Cyrpinodon v. variegatus, however, there is a tendency for the first dorsal fin ray to become thickened and spine-like but this ray remains segmented distally.

Anal Fin (Fig. 20)

The anal fin is constructed on the same general plan as the dorsal fin. The proximal radials extend in between the haemal spines and their number is usually one less than the number of the fin rays. Both median and distal radials are present.

Fin ray counts for Cyprinodon v. variegatus and other four related genera of Group I are given in Table 3.

TABLE 3

ANAL FIN RAY COUNTS FOR FIVE SPECIES OF GROUP I CYPRINODONTS

Species and Number of Species Examined	Number of Anal Rays					
	9	10	11	12	13	14
Cyprinodon v. variegatus (20)			10	10		
Floridichthys c. carpio (18)	1	17				
Jordanella floridae (18)				4	11	3
Garmanella pulchra (5)		5				
Cualac tessellatus (4)			1	3		

Pelvic Girdle (Fig. 21)

The pelvic girdle consists of a right and a left half and lies in the posterior abdominal region where it is embedded in the ventral abdominal muscles. Each half consists of a pelvic bone and seven fin rays which are connected directly to the posterior base of the pelvic bone. From each of the pelvic bones a horizontal process is given out mesially to overlap each other and thus bring the two bones into an intimate union. From the posterior inner aspects of each of the pelvic bones long bony process is given out to run posteriorly along with but dorsal to the fin rays.

Fin ray counts for *Cyprinodon v. variegatus* and four other related genera of Group I are given in Table 4.

TABLE 4

PELVIC FIN RAY COUNTS FOR FIVE SPECIES OF GROUP I CYPRINODONTS

Species and Number of Specimens Examined	Number of Pelvic Rays		
	6	7	8
Cyprinodon v. variegatus (23)		20	3
Floridichthys c. carpio (18)		12	6
Jordanella floridae (23)	23		
Garmanella pulchra (5)	1	4	
Cualac tessellatus (5)		5	

Pectoral Girdle (Figs. 22 and 23)

The pectoral girdle consists of a right and a left half. The primary portion of each half consists of the cleithrum, the scapula, the coracoid, the radials and the fin rays while the secondary portion consists of the posttemporal and the supracleithrum.

Each half of the pectoral girdle lies immediately behind the skull and is located in such a manner so that portions of the cleithrum, the supracleithrum and the posttemporal are covered by the opercle of its side. The pectoral girdle is connected with the skull on either side by the forked posttemporal. Portions of the cleithrum and the coracoid lie below the skull where they meet similar bones of the other side in the midventral line and thus form a floor under the branchial skeleton. Prominent muscles originate from the expanded lower portions of the cleithra and are inserted on the posterior half of the urohyal.

The cleithrum is elongate; its lower portion is suspended under the head, and its upper portion is produced into a cleithral process of variable extent in the five genera of cyprinodonts under discussion. In Cyprinodon v. variegatus the cleithral process is much expanded while in Jordanella floridae it is comparatively less expanded. In Floridichtys carpio and Garmanella pulchra the cleithral process is somewhat pointed and forms a hook around the pectoral base. In the former species the hook is nearer to the pectoral base than it is in the latter species. In Cualac tessellatus the cleithral process is rather small and little modified. Below the cleithral process lies a prominent scale-like bone which may be termed the subcleithral (postcleithral?) bone (Figs. 1 and 22). A prominent ridge runs the entire length of the outer surface of the cleithrum. The portion of the cleithrum anterior to this ridge is concave and situated at a lower level than the remainder of the bone. The anterior portion of the cleithrum is covered over by the posterior margin of the opercle bone. The scapula is roughly rectangular, joins the cleithrum below the cleithral process and contains a prominent scapular foramen towards its anterior extremity. A space separates the lower end of the cleithrum and the coracoid. In *Cyprinodon v. variegatus* and *Floridichthys c. carpio* there are four distinct radials, or actinosts, near the posterior margins of the coracoid and the scapula. In *Jordanella floridae*, *Garmanella pulchra* and *Cualac tessellatus*, however, only three distinct actinosts are present because the uppermost is fused with the coracoid.

The pectoral fin ray counts in *Cyprinodon v. variegatus* and and other four related genera of Group I are given in Table 5.

TABLE 5

PECTORAL FIN RAY COUNTS FOR FIVE SPECIES OF GROUP I CYPRINODONTS

Species and Number of Specimens Examined	Number of Pectoral Rays								
	12	13	14	15	16	17	18	19	20
Cyprinodon v. variegatus (16)		1	1	5	7	2			
Floridichthys c. carpio (16)							6	8	2
Jordanella floridae (18)			8	8	2				
Garmanella pulchra (5)					2	2	1		
Cualac tessellatus (2)	1	1							

Summary of Significant Osteological Characters of Group I

Ethmoid Region

(1) Mesethmoid present and composed of double laminae.

(2) Vomer edentulous.

Orbitotemporal Region

(3) Parietals absent.

(4) Inner processes of the parasphenoid present.

(5) Posterior myodome absent.

(6) Interorbital area of the frontals triangular; supraorbital area small and slightly convex dorsally.

(7) Postorbital broad.

Occipital Region

(8) Occipital region in intimate union with the first vertebra.

(9) A distinct gap between the first and second vertebra present.

(10) Articulation of the skull with the first vertebra chiefly by the basioccipital condyle of the former and the neural arches of the latter.

(11) Exoccipital condyles absent.

(12) Both the supraoccipital and the exoccipitals contributing to the formation of the foramen magnum.

(13) Supraoccipital extending backward to form a dome-shaped structure over the foramen magnum.

(14) Exoccipitals not meeting over the foramen magnum because they are separated by the dome-shaped portion of the supraoccipital.

Visceral Skeleton

(15) Metapterygoid absent.

(16) Teeth tricuspid, uniserial except for an occasional tooth or two outside the main row.

(17) Premaxillary processes small and not extending over the mesial processes of the maxillae.

(18) Outer process of the maxilla more prominent than the mesial process.

(19) Branchiostegals arranged in two groups of six pairs in Cyprinodon, and five pairs in the other genera of Group I.

Visceral Skeleton--Continued

(20) Third and fourth pharyngobranchials fused into one plate.

(21) Two ossified basibranchials.

Other Regions

(22) Posttemporal forked.

(23) Transverse processes of the precaudal vertebrae small and blunt but with prominent concavities distally for articulation with ribs.

(24) Median hypural consisting of a single fan-shaped piece

(25) Posteriorly directed bony processes of the pelvic bones elongated.

(26) Subcleithral (postcleithrum?) bone present.

(27) Haemal canals narrow.

(28) Prezygapophyses small.

(29) Supracleithrum present.

(30) Space between the cleithrum and the coracoid narrow.

GROUP II

Composition, Range and Habitat

The geographic range of this group includes countries around the Mediterranean Sea, the Red Sea and the Arabian Sea (including the Persian Gulf) up to the Gulf of Kutch.

The following genera are included:

Aphanius Nardo. About eight species.

Range: southern Europe, northern Africa and Asia Minor.

Habitat: fresh, brackish and marine littoral waters.

Aphaniops Hoedeman. Monotypic.

Range: Red Sea coast, the adjoining coast of the Indian Ocean as far as Kutch and the Mediterranean Sea.

Habitat: fresh, brackish and marine littoral waters.

Anatolichthys Kosswig and Sozer. Three species.

Range and habitat: certain lakes of Turkey.

Kosswigichthys Sozer. Monotypic.

Range and habitat: confined to Lake Hazer in eastern Turkey.

Osteology
(Figs. 24, 25 and 26)

The following species of Group II have been studied: *Aphanius cypris* (Heckel), *Aphanius sophiae* (Heckel), *Aphanius fasciatus* (Cuvier and Valenciennes), *Aphanius chantrei* (Gaillard), *Aphaniops dispar* (Ruppell), and *Anatolichthys transgrediens* Aksiray.

The osteology of these species is much like that of *Cyprinodon v. variegatus*.

Ethmoid region

The nasals, the lateral ethmoids, and the vomer are normally positioned. There is no ethmoid ossification and consequently the mesethmoid is cartilaginous.

Orbitotemporal region

The orbitotemporal region lacks parietals. The frontals are prominent and the supraorbital processes are comparatively well-developed. Posteriorly these processes enclose between themselves and the sphenotic processes small notches for the postorbitals. The postorbitals are very small in *A. phanius chantrei*, *A. phanius sophiae*, and *Anatolichthys transgrediens*, but in *A. phanius cypris*, *A. phanius fasciatus* and *Aphaniops dispar* these bones are more prominent. The postorbital is boat-shaped and has an open groove for the lateral line sensory canal. The lachrymal is normally disposed. The alisphenoids are present on either side of the cranium. The parasphenoid is normally located, its inner processes are small and do not extend laterally to join the alisphenoids.

Otic region

The otic bones are disposed as in Group I cyprinodonts and the opisthotics are absent.

Occipital region

The occipital region is composed of the usual four bones, the supraoccipital, the basioccipital and the exoccipitals. However, the supraoccipital varies in its disposition in these cyprinodonts. With the exception of *Aphanius sophiae* and *Anatolichthys transgrediens*, in which the supraoccipital extends posteriorly toward the foramen magnum and forms a small roof over it, the other species of *Aphanius* under discussion plus *Aphaniops* and *Kosswigichthys* have a supraoccipital which stops short of reaching the foramen magnum. Thus it is the exoccipitals (except in *Aphanius sophiae* and in *Anatolichthys transgrediens*) which make a major contribution to the side walls and roof of the foramen magnum. This is in contrast to the New World cyprinodontids in which the supraoccipital takes a considerable share in the formation of the foramen magnum by forming a dome-shaped structure over it.

Both the basioccipital and the exoccipitals bear condyles for articulation with the first vertebra. This is in contrast to *Cyprinodon* and its allies in which the exoccipital condyles are absent. The structure of the neural spine of the first vertebra varies in these species of cyprinodonts. In *Aphanius chantrei* and in *Anatolichthys transgrediens* there is a distinct neural spine while in *Aphanius sophiae*, *Aphanius fasciatus*, *Aphanius cypris* and *Aphaniops dispar* the tips of the transverse processes of the first vertebra are separate, although a transverse bony septum connects them below the tips. In *Kosswigichthys asquamatus* there is no neural spine because the neural arches are separate throughout and fail to meet above the neural canal.

Moreover, in contrast to Cyprinodon and its relatives, the neural arches of the first vertebra in species of cyprinodonts under discussion are separate from the occipital region and take no part in the articulation of the skull with the vertebral column.

Visceral skeleton

The quadrate and the autopalatine are disposed as in Cyprinodon. The metapterygoid is absent, and a thin mesopterygoid is applied to the quadrate and the autopalatine from behind.

The articular, the angular, and the toothed dentary are arranged as in Cyprinodon. In the upper jaw, the maxillae and the premaxillae are normally disposed. The premaxillary processes are small, and the outer process of the maxilla are better developed than its mesial process.

In Kosswigichthys asquamatus the teeth are unicuspid, blunt at their tips and arranged in a band on both the premaxilla and the dentary. In all the other species in Group II, however, the teeth are tricuspid with the middle cusp the longest, and arranged in a single row. The middle cusp, moreover, is conical in contrast to the New World cyprinodontids, in which this cusp is flat.

The hyomandibular, the symplectic, and the hyoid cornu are normal. The hypohyal is represented by a single piece on each side.

In Aphanius fasciatus and Aphaniops dispar, there are five branchiostegals which are arranged in two groups. The first group contains one ray and the second group has four. The other species, *Aphanius cypris*, *Aphanius chanterei*, *Aphanius sophiae*, *Anatolichthys transgrediens* and *Kosswigichthys asquamatus*, have four rays in the second group and none in the first.

The branchial skeleton consists of five arches having the usual number of segments. There are only two ossified basibranchials. The fourth ceratobranchial is toothed in *Aphanius cypris*, *Aphanius chanterei*, *Aphanius fasciatus*, and *Kosswigichthys asquamatus*. In *Aphanius sophiae* and *Aphaniops dispar* the fourth ceratobranchial is without teeth. The first pharyngobranchial is cartilaginous while the other three are ossified and bear teeth. The second pharyngobranchial is separate, although closely applied to the third and fourth pharyngobranchials which are, however, fused into a single plate. The basihyal and the urohyal are normal.

The posttemporal is forked in all the species of *Aphanius* under discussion and in *Aphaniops dispar*. It is unforked, however, in both *Anatolichthys transgrediens* and *Kosswigichthys asquamatus*.

Summary of Significant Osteological Characters of Group II

Ethmoid Region

(1) Mesethmoid cartilaginous.

(2) Vomer edentulous.

Orbitotemporal Region

(3) Parietals absent.

(4) Posterior myodome absent.

(5) Inner processes of the parasphenoid small and not in contact with alisphenoids.

(6) Postorbital small in *Aphanius sophiae*, *Aphanius chanterei*, *Anatolichthys transgrediens* and *Kosswigichthys asquamatus* but prominent in *Aphanius fasciatus*, *Aphanius cypris* and *Aphaniops dispar*.

Occipital Region

(7) Foramen magnum formed chiefly by the basioccipital and exoccipitals except in *Aphanius sophiae* and *Anatolichthys transgrediens* in which the supraoccipital extends backward to form a small roof over it. In no species of Group II, however, does the supraoccipital form a dome-shaped structure over the foramen magnum comparable to the one found in New World cyprinodontids.

(8) Both the basioccipital and exoccipital condyles well developed.

(9) Articulation of the first vertebra and the skull by the basioccipital and exoccipital condyles.

Occipital Region--Continued

(10) First vertebra bearing toward its anterior end two prominent, concave, articulating facets for the exoccipital condyles; neural arches of the first vertebra separate from the occipital region. The tips of the first vertebra separate in Aphanius sophiae, Aphanius fasciatus, Aphanius cypris and Aphaniops dispar although a transverse bony spetum connects the transverse processes below the tips. In Anatolichthys transgrediens and Aphanius chanterei, distinct neural spine present on the first vertebra. In Kosswigichthys asquamatus neural spine absent because the neural arches of the first vertebra fail to meet above the neural canal.

Visceral Skeleton

(11) Matapterygoid absent.

(12) Teeth tricuspid; middle cusp longest; teeth in a single row except in Kosswigichthys asquamatus in which the teeth are unicuspid, are arranged in a band, and are blunt at their distal extremities.

(13) Premaxillary processes small and pointed at the tips.

(14) Outer process of the maxilla better developed than the mesial process.

(15) Hypohyal a single piece on each side.

(16) Five pairs of branchiostegals in Aphanius fasciatus and Aphaniops dispar; four pairs in the other species.

Visceral Skeleton--Continued

(17) Third and fourth pharyngobranchials fused.

(18) Two ossified basibranchials.

Other Regions

(19) Posttemporal forked in all the species of *Aphanius* and in *Aphaniops dispar*; unforked in *Anatolichthys transgrediens* and *Kosswigichthys asquamatus*.

(20) Transverse processes of the precaudal vertebrae elongated.

(21) Median hypural consisting of a single fan-shaped piece.

RELATIONSHIPS OF GROUPS I AND II

Regan (1911) included both the New World and the Old World genera related to *Cyprinodon* and *Aphanius* in the subfamily Cyprinodontinae. In diagnosing the subfamily he pointed out that its members possess exoccipital condyles and tricuspid teeth but lack parietals. He (*op. cit.*: 523) further stated that the Cyprinodontinae "Differ from the Fundulinae only in the tricuspid teeth and the absence of parietals."

Hubbs (1926) mentioned that parietals were present in *Cyprinodon bovinus* and *Floridichthys carpio* and Myers (1931) maintained that the parietals were present in *Cyprinodon variegatus riverendi*. Concerning the presence of the basisphenoid in the latter species and in *Floridichthys carpio*, Myers (*op. cit.*: 252) wrote that the "Basisphenoid [is] present, at least in *F. carpio*." On the basis of the remarks by Hubbs and his own observations of the parietals, Myers thought that the tricuspid teeth were the only diagnostic character of the subfamily Cyprinodontinae. In this connection he (*loc. cit.*) remarked that "The tricuspid teeth distinguish this group from all others here considered. Aside from this they [Cyprinodontinae] appear to differ little from the Fundulinae." Consequently in 1931, he included *Cyprinodon*, *Floridichthys*, *Jordanella*, *Aphanius* and *Tellia* in the subfamily Cyprinodontinae but Hoedeman (1951) has since synonymized *Tellia* with *Aphanius*.

Meanwhile Kosswig and Sozer (1945) described a new genus, Anatolichthys, from Turkey and because of its tricuspid teeth it usually has been included in the subfamily Cyprinodontinae (Steinitz, 1951; Miller, 1956). Another new Turkish genus, Kosswigichthys, described by Sozer (1942), has unicuspid teeth and therefore was first thought to be a member of the subfamily Fundulinae. However, experimental hybridization and cytological studies by Aksiray (1952) and Oztan (1954) produced strong evidence that Kosswigichthys actually is more closely related to Aphanius and Anatolichthys despite the fact that both of these latter genera have tricuspid teeth.

Miller (1956: 3) while discussing the relationships of Cualac, a Mexican genus with tricuspid teeth, remarked that "Cualac may well be closely related to Fundulus, with conical teeth, as to the cyprinodontids, with tricuspid teeth." He proposed, therefore, that the two subfamilies Cyprinodontinae and Fundulinae be united into one subfamily Cyprinodontinae.

It has already been pointed out, in connection with the description of the osteology of Group I, that the New World genera with tricuspid teeth lack exoccipital condyles. Therefore, Regan's (1911) conclusion regarding the presence of exoccipital condyles in New World Cyprinodontinae is not correct. Since New and Old World genera with tricuspid teeth (Groups I and II) differ from one another not only in the presence or absence of exoccipital condyles, but also in other fundamental characters presently to be discussed, it is evident that in the past these two different phyletic entities have been confused under the subfamily Cyprinodontinae.

Both Hubbs (1926) and Myers (1951) appear to be in error in pointing out the presence of parietals in *Cyprinodon* and in *Floridichthys*, for in the three species of *Cyprinodon*, which I have studied and in *Floridichthys carpio*, these bones are absent. Further, the parietals are also absent in *Jordanella*, *Garmanella*, *Cualac*, *Aphanius*, *Aphaniops*, *Anatolichthys* and *Kosswigichthys*. Similarly I have found that the basisphenoid is not only absent in *Floridichthys* but it is absent also in all other cyprinodonts under consideration in this study.

Concerning the relationships of *Kosswigichthys*, the osteological evidence is in harmony with the views of Aksiray (1952) and Oztan (1954) who, on the basis of experimental hybridization and cytological studies, concluded that *Kosswigichthys* is related more closely to *Aphanius* and *Anatolichthys* which have tricuspid teeth than to *Valencia* which has conical teeth. Absence of parietals and the cartilaginous nature of the mesethmoid are the two characters which I cite in support of my interpretation of the close relationship between *Kosswigichthys* and *Aphanius*.

Miller (1955, 1956) suggested that the two subfamilies Cyprinodontinae and Fundulinae be united into one subfamily Cyprinodontinae. In this connection it might be pointed out that there are several fundamental differences between the New World cyprinodontids with tricuspid teeth (Group I) and the Fundulids with conical or bicuspid teeth (Group III). These differences relate not only to the nature of teeth but also to differences in the first vertebrae, the premaxillary processes, the maxillary processes, the occipital condyles, the posttemporals, and the parietals. Therefore, Group I and Group II represent two distinct phyletic lines easily separable from each other on the basis of major osteological differences. However, the subfamilies Cyprinodontinae and Fundulinae as delimited by Myers (1951), and as understood by most subsequent authors, contain heterogenous phyletic entities which have been confused under these groups. For example, the Old World genera, *Aphanius*, *Aphaniops*, and *Anatolichthys* (all with tricuspid teeth), and *Kosswigichthys* (with unicuspid teeth); and the New World genera, *Cyprinodon*, *Floridichthys*, *Jordanella*, *Garmanella*, and *Cualac* (all with tricuspid teeth), have been grouped under the subfamily Cyprinodontinae, although they form two phyletic entities when their osteological characteristics are considered. Similarly, as will be shown presently, the New World genera related to *Fundulus* (conical or bicuspid teeth) and the Old World genus *Valencia* (conical teeth) also possibly form two separate phyletic entities and should not be grouped together in the same subfamily as has been the practice in the past. Therefore, in order to make the classification of the genera now grouped under two subfamilies Cyprinodontinae and Fundulinae, a natural one, four groups should be recognized. They are:

(a) The New World genera with tricuspid teeth
(b) The Old World genera with tricuspid or unicuspid teeth
(c) The New World genera with conical or bicuspid teeth
(d) The Old World genus *Valencia* with conical teeth

This grouping of genera was anticipated by both Hoedeman (1951) and Miller (1955, 1956). Hoedeman (1951: 1), while attempting a rediagnosis of the Old World cyprinodont genus Aphanius, remarked: "We found the Old World genera and species . . . to be closely related, and doubtless forming a phyletic unity, quite well separable from the New World genera of this subfamily [Cyprinodontinae]." Hoedeman (1951: 1-2) separated the New and the Old World genera in two tribes, Aphaniidi and Cyprinodontidi, and listed the following characters distinguishing them:

"I. Teeth tricuspid, middle cusp the longer, usually sharply pointed, side cusps small; preorbital margin rather narrow, usually one-half eye diameter or less, but not as narrow as in Rivulidi; preorbital [premaxillaries?] not firmly united, in contact with each other for only one third or less of the inner margin, the backward directed processes narrow, . . . tribe Aphaniidi Hoedeman, 1949.

II. Teeth tricuspid, middle cusp not always the longer, usually spatulate, not pointed as in Aphaniini; preorbital margin more than one-half eye diameter; premaxillaries firmly united, in contact with each other for nearly the entire inner margin, the backward directed processes rather broad . . . tribe Cyprinodontidi Hoedeman, 1949."

Miller (1955: 11) remarked about Valencia, of the fresh waters of Spain: "An examination of specimens of Valencia hispanica and syntypes of V. letourneuxi convinces me that this genus is a generalized, independent derivative probably not closely related to any New World genus." Again while discussing the relationships of the genus Cualac, Miller (1956: 9) commented: "It is entirely possible that the Old World genera with tricuspid teeth have been independently derived from ancestors there and are not intimately related to their New World representatives."

The results of the current study tend to support the conclusions of Hoedeman (1951) and Miller (1955, 1956) concerning the independent derivation of the Old World aphanids, valencids, and the New World cyprinodontids and fundulids from ancestors in their respective areas. Since no conclusive evidence has been advanced previously in support of the independent derivation of the Old World and New World cyprinodonts with tricuspid teeth, the osteological characters in which the two groups differ from each other are listed in Table 6.

A perusal of the list of differences shown in Table 6 makes it evident that the Old World genera (Aphanius, Aphaniops, Anatolichthys and Kosswigichthys) differ markedly from those of the New World (Cyprinodon, Floridichthys, Jordanella, Garmanella, and Cualac). Further, the Old World genera under consideration appear to be more closely related to geographically widespread aplocheilids than to the New World genera. This relationship is based upon the fact that both the aplocheilids (to be described later) and the members of the Old World genera possess exoccipital condyles, have a cartilaginous mesethmoid, and similar first vertebrae.

One possible explanation for this relationship is that some ancestral aplocheilid-like stock gave rise, in the Old World, to the genus Aphanius or Aphaniops which in turn produced Anatolichthys and Kosswigichthys. More recently Konuralp (1955: 117) from a study of

TABLE 6

COMPARISON OF NEW WORLD GENERA (GROUP I) AND OLD WORLD GENERA (GROUP II) OF CYPRINODONTS

New World Genera (Group I) (*Cyprinodon*, *Floridichthys*, *Jordanella*, *Garmanella*, and *Cualac*)	Old World Genera (Group II) (*Aphanius*, *Aphaniops*, *Anatolichthys* and *Kosswigichthys*)
Exoccipital Condyles	
Absent	Present
Foramen Magnum	
Formed by basioccipital, supraoccipital and exoccipitals	Formed almost entirely by basioccipital and exoccipitals
Supraoccipital	
Extends posteriorly to form a conspicuous dome-shaped structure over the foramen magnum	Rarely reaches the foramen magnum and never forms more than a minor and almost imperceptible portion of its roof
Mesethmoid	
Ossified and composed of double laminae	Cartilaginous
First Vertebra	
Articulates with skull by the basioccipital condyle and neural arches	Articulates with skull by the basioccipital and exoccipital condyles
Neural arches applied to or even ossified with occipital region	Neural arches separate from skull
No distinct gap between first and second vertebrae	Distinct gap between first and second vertebrae

embryonic development of the gonads and their relationships to other organs in four species of *Aphanius*, *Kosswigichthys asquamatus*, and *Anatolichthys transgrediens* concluded that *Anatolichthys*, *Kosswigichthys*, and *Aphanius chanterei* have arisen as a result of hybridization.

GROUP III

Composition, Range and Habitat

Group III is confined to the New World and, except for a few forms found in Bermuda, Cuba and Jamaica, its representatives occur mainly in North and Central America. The following genera are included: *Fundulus*, *Adinia*, *Lucania*, *Chriopeops*, *Leptolucania*, *Empetrichthys*, *Crenichthys*, *Profundulus*, *Cubanichthys*, *Chriopeoides*, *Oxyzygonectes* and *Hubbsichthys*.

Fundulus Lacepede. About 35 currently recognized species and subspecies.

Range: southeastern Canada, most of the United States, the Bermuda Islands, Cuba, and Gulf coastal areas of Mexico as far south as the Yucatan Peninsula.

Habitat: fresh and salt water from upland streams to marine littoral situations.

Adinia Girard. Monotypic.

Range: Gulf Coast of the United States from Florida to Texas.

Habitat: shallow lagoons along the coast.

Lucania Girard. Monotypic.

Range: along the Atlantic Coast from Connecticut to Mexico.

Habitat: brackish water, invading fresh water for some distance.

Chriopeops Fowler. Monotypic.

Range: endemic to Florida.

Habitat: small ponds, streams, and ditches.

Leptolucania Myers. Monotypic.

Range: southern Georgia and Florida eastward from the Appalachicola River Basin.

Habitat: fresh water swamps, streams and ditches.

Empetrichthys Gilbert. 2 species.

Range: confined to the Death Valley region of Nevada.

Habitat: desert warm springs, frequenting the deeper holes; usually uncommon in shallow spring-fed ditches or marshy areas.

Crenichthys Hubbs. 2 species.

Range: restricted to Central Nevada.

Habitat: warm springs.

Profundulus Hubbs. 5 species.

Range: along both slopes of Middle America from near Acapulco, Mexico, to western Honduras on the Pacific side and from the Isthmus of Tehuantepec to Rio Motagua, Guatemala, on the Atlantic slope.

Habitat: restricted to fresh water and typically inhabiting the mountain streams of Middle America where they are most abundant at altitudes between 3,000 and 7,000 feet.

Cubanichthys Hubbs. Monotypic.

Range: appears to be confined to the island of Cuba.

Chriopeoides Fowler. Monotypic.

Range: Jamaica.

Oxyzygonectes Fowler. Monotypic.

Range: along the Pacific Coast of Costa Rica.

Habitat: salt and brackish waters.

Osteology

The account is based on a study of sixteen species representing eight of the eleven genera comprising the group. Representatives of the genera *Cubanichthys*, *Chriopeoides* and *Oxyzygonectes* were not available. The species studied are listed below:

Fundulus chrysotus (Gunther), *F. grandis* (Baired and Girard), *F. similis* (Baired and Girard), *F. confluentus* Goode and Bean, *F. notti* (Agassiz), *F. cingulatus* Cuvier and Valenciennes, *F. olivaceus* (Storer), *F. kansae* Garman; *Adinia xenica* (Jordan and Gilbert); *Lucania parva* (Baired and Girard); *Chriopeops goodei* (Jordan); *Leptolucania ommata* (Jordan); *Empetrichthys latos* Miller; *Crenichthys nevadae* Hubbs, *Crenichthys baileyi* (Gilbert); *Profundulus hildebrandi* Miller.

Head Skeleton

The head skeletons (Figs. 27, 28, 29 and 30) of the genera in Group III compare favorably with that of *Cyprinodon* except for certain structural differences and the presence of additional bony elements.

These additional elements and differences will be emphasized in the following discussion which relies on the previously given description of Cyprinodon for comparison and reference.

The head skeleton in these genera is longer than deep. The skull is uniformly broad due to the development of prominent supraorbital processes of the frontals. These processes are flat and completely cover the eyes from above. The interorbital width in the middle orbital region is about the same as between the outer edges of the pterotics except in Lucania, Chriopeops and Leptolucania where the interorbital region is narrow. The orbitotemporal region has a pair of distinct parietals. The premaxillary processes are elongated and extend posteriorly over the mesial processes of the maxillae. The epiotics bear posteriorly directed epiotic processes of variable extent. The epiotic processes are absent, however, in Adinia and Leptolucania. The neural arches of the first vertebra in all the genera under consideration are separate from the skull.

The general shapes of the skulls and their proportions suggest three distinct evolutionary trends in the genera of Group III. The details and the phylogenetic significance of these three trends will be discussed after the osteology of these genera has been presented.

Skull

The skull (Figs. 51, 52, 53 and 54) will be described under the same four headings used for Cyprinodon: ethmoid region, orbitotemporal region, otic region, and occipital region.

Ethmoid region

The ethmoid region is similar in most respects to that of Cyprinodon and the genera closely related to it, insofar as the number and disposition of bones and cartilages are concerned. The major differences relate to the mesethmoid and the vomer.

As compared to Cyprinodon, the mesethmoid is more prominent in all these genera. It is situated in the anterior ethmoid cartilage, is closely applied to the dorsal surface of the vomer and is composed of double laminae. The mesethmoid in Profundulus, Empetrichthys and Crenichthys (Fig. 35C) is large and comes in contact with the lateral ethmoids on both sides. In the remaining genera, Fundulus, Adinia, Lucania, Chriopeops and Leptolucania, the mesethmoid is small and does not come in contact with the lateral ethmoids.

The vomer in Profundulus, Empetrichthys, Crenichthys, Adinia and Leptolucania fails to meet the lateral ethmoids. In Fundulus, Lucania and Chriopeops, on the other hand, the vomer comes in contact with the lateral ethmoids through its posterolateral processes.

Orbitotemporal region

The orbitotemporal region has a pair of parietals which are situated obliquely on either side of supraoccipital and immediately behind the frontals. Anterolaterally each parietal comes in contact with the sphenotic and the pterotic while posteriorly it is in contact with the epiotic and the supraoccipital.

The frontals occupy the same position as in Cyprinodon. In Profundulus, Fundulus, Empetrichthys, Crenichthys and Adinia the supraorbital processes of the frontals are well developed, flattened dorsally and cover the eyes completely. In Lucania, Chriopeops and Leptolucania, on the other hand, the supraorbital processes are less well developed, are convex dorsally, and do not cover the eyes completely.

The parasphenoid is similar to the one in Cyprinodon except for its anterolateral processes, which in Profundulus, Fundulus, Empetrichthys and Crenichthys extend laterally to meet similar extensions from the alisphenoids to enclose a posterior myodome on each side.

The posterior myodome is formed in three different ways in the several genera under consideration: 1. In Empetrichthys latos, Fundulus cingulatus, and Fundulus kansae, the anterolateral process of the parasphenoid meets a process form the alisphenoid on each side and thus enclose a rather wide myodome; in these species the prootic does not contribute to the formation of this structure as it does in Profundulus, Crenichthys, and several species of Fundulus. 2. In Fundulus notti, the anterolateral process of the parasphenoid meets the mesial process of the prootic to enclose a myodome and there is no connection between the parasphenoid and the alisphenoid. 3. In Profundulus hildebrandi, Crenichthys nevadae, Crenichthys baileyi, Fundulus chrysotus, F. grandis, F. similis, F. confluentus, and F. olivaceus the anterolateral process of the parasphenoid meets an extension of the alisphenoid on each side; in addition, the prootic sends a small anteromesial process which joins from behind the extensions of the parasphenoid and the alisphenoid at a place where the latter join one another. In this manner a comparatively small myodome is enclosed internal to these processes.

In *Adinia*, *Lucania*, *Chriopeops*, and *Leptolucania* the posterior myodome is absent. In these genera the alisphenoids have no connection with the anterolateral processes of the parasphenoid which, as in *Cyprinodon* and its allies, are located on the inner aspect of the parasphenoid. A few minor modifications are to be noted in this connection. In *Adinia* a mesial extension of the prootic is present, although neither this extension nor the anterolateral process of the parasphenoid and the alisphenoid join one another. In *Lucania*, although the anterolateral process of the parasphenoid does not join the alisphenoid, a mesial extension of the prootic joins the alisphenoid.

Both the lachrymal and the postorbital are normally disposed. The postorbital lies in a notch of the frontal which is positioned in the posterior corner of the skull where it is wedged between the well developed supraorbital process of the frontal and the sphenotic. The postorbital is more anteriorly placed than that of *Cyprinodon*, and takes part in forming the posterior boundary of the orbit. The postorbital lies anterior to the sphenotic; in contrast it lies external to the latter bone in *Cyprinodon*. The postorbital is a boat-shaped bone with an open sensory canal on its external surface.

The lachrymal in *Empetrichthys* and *Crenichthys* is narrower than in the other genera under discussion. Both the basisphenoid and the orbitosphenoids are absent.

Otic region

The otic region is similar to that of Cyprinodon in almost all essential respects. There are, however, a few differences in details.

In several genera the epiotics bear posteriorly directed epiotic processes on their posterior dorsal extremities. These processes are large and branched at their distal extremities in all the species of Fundulus under consideration and also in Profundulus hildebrandi; small to fairly prominent in Chriopeops; small and pointed (9 specimens) to absent (9 specimens) in Lucania; small and stumpy in both species of Crenichthys, Empetrichthys latos; and absent in Adinia and Leptolucania.

The prootic is prominently developed and sends an anteromesial process which, along with the anterolateral process of the parasphenoid and the alisphenoid, contributes to the formation of the previously described posterior myodome. In Empetrichthys latos and two species of Fundulus, F. cingulatus and F. kansae, however, the anteromesial process of the prootic is lacking. In the other six species of Fundulus, in both the species of Crenichthys and in Profundulus hildebrandi, an anteromesial process of the prootic is present. In Chriopeops and Leptolucania neither the parasphenoid, the alisphenoid or the prootic extends mesially to join each other. In Adinia, although an anteromesial process of the prootic is present and the anterolateral processes of the parasphenoid and the alisphenoid are prominent, none of these processes join one another. In Lucania the anteromesial process of the prootic joins the alisphenoid but the anteromesial limb of the parasphenoid and the alisphenoid are separate. Other features of the prootic are similar to those of Cyprinodon. This is also true of the pterootic and the sphenotic. As in Groups I and II, the opisthotics are absent.

Occipital region

The occipital region, as in Cyprinodon and its allies, is made up of four bones, a supraoccipital, a basioccipital and two exoccipitals, which make up the posterior region of the skull. The foramen magnum is formed entirely by the basioccipital below and the exoccipitals which contribute not only the side walls but also the roof. The supraoccipital stops short of reaching the foramen magnum and, therefore, does not take part in its formation. The exoccipitals bear prominent condyles for articulation with the first vertebra (Fig. 35B). The relationships of the occipital bones with the remainder of the skull are similar to those in Cyprinodon except that, in all the genera under consideration, the supraoccipital not only comes in contact with the frontals but also with the parietals.

Unlike the situation in Cyprinodon and its allies, the neural arches of the first vertebra remain separate and are not applied to the occipital region (Fig. 44). The skull articulates with the first vertebra by both basioccipital and exoccipital condyles.

Visceral skeleton (Figs. 35A, 36B, 36C, 37, 38, 39, 40A, 40C and 41)

Mandibular arch

Except for some significant differences in the shapes of certain bones, the mandibular arch is much like that of Cyprinodon.

One difference concerns the maxilla which is consistently different from that of Cyprinodon. In Group III the outer process of the maxilla is less conspicuous, but its mesial process is better developed, more elongate, and supports the elongated premaxillary process from below (Fig. 35A). This is designated the fundulid type of maxilla in contrast to the cyprinodontid type as exemplified by Cyprinodon and its allies of Group I.

The premaxillae are produced into more elongate premaxillary processes in contrast to Cyprinodon and its allies which have small premaxillary processes. The teeth are of two types, bicuspid in Crenichthys and conical in all the other genera. Because the structure and arrangement of the teeth are useful in generic segregation, a summary is given for those species of Group III which have been examined in this study (Table 7).

Hyoid arch

The bones of the hyoid arch are similar to those in Cyprinodon and the hypohyal on each side is represented by a single bony piece.

The structure and arrangement of the opercular bones resemble the pattern in Cyprinodon and its allies. The number of branchiostegals, however, differ in different genera comprising Group III as shown in Table 8.

TABLE 7

COMPARISON OF TOOTH STRUCTURE AND ARRANGEMENT OF JAW TEETH IN SEVERAL SPECIES OF GROUP III CYPRINODONTS

Species	Arrangement of Teeth on Premaxillary and Dentary
With Conical Teeth:	
Profundulus hildebrandi	Arranged in a band, outer row of large and several inner rows of small teeth
Fundulus (all eight species in this study)	Same as *Profundulus*
Adinia xenica	Same as *Profundulus*
Lucania parva	One row of conical teeth
Chriopeops goodei	Two rows of conical teeth
Leptolucania ommata	Same as *Chriopeops*
Empetrichthys latos	Outer row of large and an inner row of small teeth
With Bicuspid Teeth:	
Crenichthys baileyi	Outer row of large bicuspid and two inner rows of small conical teeth
Crenichthys nevadae	Outer row of large bicuspid and one inner row of small conical teeth

TABLE 8

NUMBER OF BRANCHIOSTEGAL RAYS IN SELECTED SPECIES OF GROUP III

Species and Number of Specimens Examined	Number of Branchiostegal Rays			
	3	4	5	6
Fundulus chrysotus (7)			7	
F. grandis (5)			5	
F. similis (4)				4
F. confluentus (6)			6	
F. notti (4)			4	
F. cingulatus (5)			5	
F. olivaceous (4)			4	
F. kansae (4)			4	
Lucania parva (16)			1	15
Chriopeops goodei (4)[†]			2	2
Leptolucania ommata (10)	10			
Empetrichthys latos (2)				2
Crenichthys baileyi (2)			2	
Crenichthys nevadae (2)			2	
Profundulus hildebrandi (4)				4

[†] In two other specimens of *Chriopeops goodei* there were 5 branchiostegals on the left half of the hyoid cornu and 6 on the right half. These were the only cases in which the counts varied from side to side in any of the species examined.

Branchial arches

The number of branchial arches and the bones composing them are similar to those of *Cyprinodon*. The differences relate chiefly to the number of gill-rakers and to the extent with which the fourth ceratobranchial is provided with teeth. There are two ossified basibranchials and four epibranchials. The first pharyngobranchial is cartilaginous and lacks teeth while the other three are ossified and bear teeth. The second pharngobranchial is separate but the third and fourth are fused into a single plate. The basihyal and the urohyal are normal.

Because characteristics associated with the pharyngeal bones have been utilized in generic segregation by several authors, these bones warrant a special mention. Gilbert (1893: Pl. 5) published a figure of the pharyngeal bones of *Empetrichthys merriami* and since then Garman (1895: 116), Hubbs (1932: 3) and Miller (1948: 99-100) have characterized the genus *Empetrichthys* solely on the nature of its pharyngeal bones. Miller (*loc. cit.*) in diagnosing the genus *Empetrichthys* reported that the "Upper and lower pharyngeal bones [are] greatly enlarged [and] the lower pharyngeals [are] completely united." He reported also that "The tubercular-shaped molar teeth and the greatly enlarged upper and lower pharyngeal bones are the most distinctive characters of the genus."

In *Empetrichthys* latos the pharyngeal bones are normal in that they are neither greatly enlarged nor are the lower pharyngeals united with one another. Moreover, the teeth on the upper and lower pharyngeals are distinctly conical. Therefore, the generic diagnosis of Empetrichthys as proposed by Garman (1895), Hubbs (1932) and Miller (1948) is untenable and requires revision. Complete diagnosis of the genus Empetrichthys, however, cannot be undertaken here due to the lack of pertinent material. In the present study the pharyngeal bones of twenty-eight genera of cyprinodonts have been examined and it was found that the use of characteristics associated with these bones have little value in separating genera. In no cyprinodont have I found the lower pharyngeals to be united completely. The lower pharyngeals are always separate although there is variation in the amount of spacing between them. The lower pharyngeals are very close together in Orestias agassizii (Group VIII) Lucania, Chriopeops, Leptolucania, Garmanella, Cualac and the aplocheilids (Group V). In all the other genera examined, including Empetrichthys, there is a distinct space between the lower pharyngeals.

The posttemporal is forked in Profundulus hildebrandi, Empetrichthys latos, both the species of Crenichthys, and Fundulus kansae. Moreover in these species, a thin membranous bony lamina extends between the lower end of the two limbs of the fork (Figs. 40B, 42 and 43). The posttemporal is unforked, however, in all the remaining species of Fundulus under consideration, as well as in Lucania, Chriopeops and Leptolucania.

Summary of Significant Osteological Characters of Group III

Ethmoid Region

(1) Mesethmoid ossified and composed of double laminae.

(2) Vomer edentulous.

Orbitotemporal Region

(3) Parietals present.

(4) Posterior myodome present except in Adinia, Lucania, Chriopeops and Leptolucania.

(5) Anterolateral processes of the parasphenoid share in the formation of the posterior myodome except in Adinia, Lucania, Chriopeops and Leptolucania.

(6) Interorbital area of the frontals rectangular, supraorbital area well developed and flattened dorsally except in Lucania, Chriopeops and Leptolucania in which the interorbital area is somewhat triangular and the supraorbital area is small and slightly convex dorsally.

Occipital Region

(7) Occipital region of the skull not in intimate union with vertebral column; no distinct gap between the first and second vertebrae.

(8) Articulation of the skull with the first vertebra is through a basioccipital and two exoccipital condyles; neural arches of the first vertebra separate and take no part in the articulation.

(9) Exoccipital condyles well developed.

(10) Foramen magnum formed entirely by exoccipitals; supraoccipital not reaching foramen magnum.

(11) Supraoccipital not forming a dome-shaped structure over the foramen magnum.

(12) Exoccipitals meet over the foramen magnum.

Otic Region

(13) Epiotic processes present in all genera examined except *Adinia* and *Leptolucania*.

Visceral Skeleton

(14) Metapterygoid absent.

(15) Teeth conical or bicuspid.

(16) Premaxillary processes of three types:

short and broad	*Profundulus*
short and narrow	*Empetrichthys* and *Crenichthys*
long and narrow	*Fundulus*, *Adinia*, *Lucania*, *Chriopeops* and *Leptolucania*.

(17) Maxilla with a well-developed mesial process and weakly-developed outer process.

(18) Hypohyal represented by a single bony piece on each side.

(19) Branchiostegals 3, 5 or 6.

(20) Third and fourth pharyngobranchials fused into one plate.

(21) Two ossified basibranchials.

Other Regions

(22) Posttemporal unforked except in Profundulus, Empetrichthys and Crenichthys; in Fundulus kansae it is forked and the processes of the fork are joined by a bony lamina towards its lower end.

(23) Transverse processes of the precaudal vertebrae elongated

(24) Posteriorly directed bony processes of the pelvic bones small.

(25) Subcleithral bone present in all the genera except Leptolucania.

(26) Haemal canals wide.

(27) Prezygapophyses prominent.

(28) Median hypural either clearly divided into parts by a suture or shows indications of such a dividion (Profundulus, Empetrichthys and Crenichthys). In other genera of Group III, median hypural is a single, fan-shaped piece with no indications of division.

Relationships of Group III

The genera which have been delimited in Group III show sufficient similarities relative to their osteological characters and geographical distribution to suggest that they form a phyletic unity. In addition, the members of Group III appear to be related to the widespread aplocheilids which are to be described later under Group V. The characters shared by members of Group III and Group V are summarized under two heads to show the points of agreement and disagreement.

1. Osteological characters common to Group III (fundulids) and Group V (aplocheilids)
    - (a) Skull long and uniformly wide.
    - (b) Parietals present.
    - (c) Interorbital area of frontals rectangular; supraorbital area well developed, dorsally flattened and covers eyes completely.
    - (d) Foramen magnum formed entirely by exoccipitals; supraoccipital not reaching the foramen magnum.
    - (e) Supraoccipital not forming a dome-shaped structure over the foramen magnum.
    - (f) Exoccipital condyles well developed.
    - (g) Articulation of the skull with the first vertebra by a basioccipital and two exoccipital condyles.
    - (h) Neural arches of the first vertebra separate from the skull.
    - (i) Teeth conical; arranged in a band; outer row large.
    - (j) Premaxillary processes short and broad.
    - (k) Maxilla with a well-developed mesial process and weakly-developed outer process.
    - (l) Posttemporal forked or unforked.
    - (m) Transverse processes of the precaudal vertebrae elongated.
    - (n) Posteriorly directed bony processes of the pelvic bones small.
    - (o) Haemal canals wide.

   (p) Median hypural either clearly divided into parts by a suture or indication of such a division evident.

2. In certain other osteological characters fundulids (Group II) differ from aplocheilids (Group V) and thus either stand apart or show resemblances to cyprinodontids (Group I). These characters are:
   (a) Mesethmoid ossified and composed of double laminae.
   (b) Vomer edentulous.
   (c) Two basibranchials.
   (d) Posttemporal forked (at least in *Profundulus*, *Empetrichthys*, *Crenichthys* and *Fundulus kansae*).
   (e) Median hypural composed of single fan-shaped piece without any indications of division.

In the structure of the first vertebra the fundulids are entirely and consistently different from all other cyprinodonts which I have examined. The neural arches of the first vertebra in the fundulids are separate from the occipital region and never meet above the neural canal to form a neural spine. In *Produndulus*, and in some specimens of *Crenichthys baileyi* there is, however, a thin bony septum which connects the neural arches of the first vertebra just below their separate tips. Although no such bony septum connects the neural arches of the first vertebra in each of the two specimens of *Crenichthys nevadae* and *Empetrichthys latos* which I have cleared and stained, it is possible that an examination of a larger series of these two species might reveal a first vertebra of the type found in *Profundulus* and *Crenichthys baileyi*.

It is apparent from the list of osteological characters given above that the New World fundulids (Group III) show a close relationship to the widespread aplocheilids (Group V) on the one hand and to the New World cyprinodontids (Group I) on the other. The distribution of the aplocheilids (Group V) is a southerly one, principally African, South American and to some extent South Asian. This southerly occurrence resembles the southern, peripheral distribution of the more primitive members of many groups of terrestrial and fresh water vertebrates and invertebrates. Moreover, as will be shown in connection with the description of Group V, the aplocheilids present by far the largest number of basic osteological and other characters that have become specialized or even lost in other groups. Thus in the fundulids (Group III) under discussion, an ossified mesethmoid composed of double laminae seems to be a modification of the cartilaginous mesethmoid found in the aplocheilids. Similarly, the first vertebra of the fundulids is without a neural spine and may well have been derived from that of some aplocheilid-like stock which had a normal first vertebra and neural spine. After the evolution of a vertebra in which the neural arches do not meet above the neural canal to form a neural spine, it is easy to visualize further modifications of the first vertebra leading to the condition found in <u>Cyprinodon</u> and its allies (Group I). For example, in a fundulid-like stock with 'free' neural arches it could be supposed that these arches became applied to the occipital region as functional articulations. These articulations would then provide the type of skull-vertebral column relationship found in Group I especially in the event of subsequent loss of the exoccipital condyles and the parietals.

Another structure in fundulids which seems to be a modification from the aplocheilids relates to the median hypural. The median hypural is a bifid or trifid structure in the aplocheilids while in the fundulids it is a single fan-shaped element except that in certain genera (Profundulus, Empetrichthys and Crenichthys) it still shows indications of a bifid nature.

The lack of vomerine teeth and the absence of a metapterygoid may be mentioned as an example of the structures which have been lost in fundulids but are still present in aplocheilids.

Thus both the distributional and the osteological evidence indicate that the aplocheilids gave rise to the fundulids and that in their turn, the fundulids produced the New World cyprinodontids. These and related matters will be discussed more fully following the description of the osteological characters of all the groups under consideration.

Evolutionary Trends Within Group III

Within Group III two, and possibly three, evolutionary lines are apparent on the basis of osteological characters. As was mentioned earlier, the general shape of the skull and its proportions suggest three evolutionary trends in the genera included in Group III. These trends are:

(1) In Profundulus, Empetrichthys and Crenichthys, the supraorbital processes of the frontals are well developed and cover the

eyes completely, the epiotics are broad and slope gradually toward the pterotics which lie at about the same level as the epiotics.

(2) In Fundulus and Adinia although the supraorbital processes are well developed and cover the eyes completely, the epiotics are narrow, constricted in the middle and form a distinct epiotic crest on both sides; the pterotics lie at a considerably lower level than the epiotics.

(3) In Lucania, Chriopeops and Leptolucania, in addition to a similar disposition of epiotics and pterotics as in Fundulus and Adinia, the supraorbital processes of the frontals are less developed, they are slightly convex dorsally and fail to cover the eyes completely. Moreover, in these three genera, the interorbital width in the middle orbital region is less than between the outer edges of the pterotics.

Further, it becomes all the more clear that Profundulus, Empetrichthys and Crenichthys form a phyletic unity within the group, when it is considered that these three genera seem to share many fundamental characters and that these same characters are absent in all the other genera of the group under consideration. These characters are:

(a) The genital pouch is either absent or obsolete (absent in Empetrichthys and Crenichthys and weak to obsolete in Profundulus).

(b) The dorsal and anal fins are posterior (the origin of the dorsal being over or almost over that of the anal) and except for the pelvic fins (absent in Empetrichthys and Crenichthys) all fin ray counts overlap.

(c) Premaxillary processes are short and wide in Profundulus, short and narrow in Empetrichthys and Crenichthys, while in all the other genera of Group III these processes are typically long and narrow.

(d) The gill-rakers are numerous, about 14 in Empetrichthys, about 16 to 18 in Profundulus and about 27 in Crenichthys while in all the other genera of Group III (except for Adinia which has about 16), the number of gill-rakers is about 6.

(e) Mesethmoid is large and in contact with the lateral ethmoids.

(f) Vomer is not in contact with the lateral ethmoids.

(g) Median hypural is either clearly divided into two parts by a suture or shows indications of such a division.

(h) Posttemporal is forked and the two limbs of the fork are united by a bony lamina toward their lower ends.

(i) Number of vertebrae is usually more than the other genera of Group III: 28 in Crenichthys baileyi, 31 in Empetrichthys latos, 36 in Profundulus hildebrandi and according to Miller (1955 : 11) Profundulus has 31 to 39.

(j) Neural arches of the first vertebra do not meet above the neural canal to form a neural spine, but a transverse bony septum connects the neural arches just below their tips.

Although Profundulus of the Mexican Plateau currently shows a disjunct distribution with Empethrichthys and Crenichthys of Death Valley, Nevada, this, as in many other primitive forms, may not have been always the case. In this connection the following remarks of Miller (1955: 16) seem pertinent: "We cannot be certain, for example, that Fundulus detillai and Fundulus sternbergi, as described by Hibbard and Dunkle (1942) and Robertson (1943), respectively, from the Middle Pliocene of Kansas, may not belong to Profundulus."

This would indicate that the genus Profundulus or, more probably, a stock similar to it was distributed from the Mexican Plateau to Death Valley, at least in the middle Pliocene or even earlier. This stock differentiated on the one hand into such closely related genera as Profundulus, Empetrichthys and Crenichthys and on the other into Fundulus. From the latter were derived two stocks: Cyprinodon and its allies (Group I), and the Adinia-Lucania group. Lucania parva, Chriopeops goodei (Lucania goodei of several recent authors) and Leptolucania ommata are closely related forms and it is suggested that Lucania parva, which ranges along the Atlantic Coast from Connecticut to Mexico and enters the fresh waters of Florida, may have differentiated in Florida to form two strictly fresh water species Chriopeops goodei and Leptolucania ommata.

Although the foregoing phyletic trends are suggested by the present findings, a more exhaustive study is required to determine the precise relationships of various genera in Group III. More information is needed concerning the fossil record, a more thorough coverage of representative species especially in the genera Fundulus and Profundulus is necessary, and, in all the forms, more data are required on the comparative osteology, embryology and anatomy of the soft parts.

Relationships of Empetrichthys

Before concluding the part on the relationships of Group III, it is worthwhile to comment separately upon the relationships of Empetrichthys because they have been confused in the past. In his original description Gilbert (1893: 233-234) commented that Empetrichthys "seems most closely allied to Orestias, of which numerous species have been described from lakes in high Andes of South America." Garman (1895: 116) regarded the genus as "allied to Fundulus through the more compressed species." Jordan and Evermann (1896: 631, 667) placed Empetrichthys in the subfamily Orestiinae and Eigenmann (1920) seemed equally impressed by the rather close superficial resemblance of Empetrichthys and Orestias when he commented: "They are so similar that they might be regarded as forming but one genus." Similarly Jordan (1923: 158) listed Empetrichthys and Orestias as the only members of the family Orestiidae and thereby indicated their close relationship. Jordan, Evermann, and Clark (1930: 182) erected a separate family, Empetrichthydae, for the sole reception of Empetrichthys. Myers (1931: 10), utilizing some of the skeletal characters (simple epipleurals and the presence of parietals in Empetrichthys as against bifid or trifid epipleurals and the absence of parietals in Orestias pentlandii) concluded that: "It [Empetrichthys] appears to have nothing to do with Orestias." He placed [Empetrichthys] in the subfamily Fundulinae of the family Cyprinodontidae but left untouched the precise relationships of this genus with the other genera included in the tribe Fundulini. Hubbs (1932) while commenting upon the same problem remarked that "There is probably no immediate relationship between Empetrichthys and Orestias, although both were probably derived from some such basic stock as Profundulus." Miller (1948: 100), on the other hand, remarked differently: "Empetrichthys probably originated from Fundulus, as was suggested by Garman."

I agree with Myers (1931) that Empetrichthys and Orestias are unrelated genera, but his use of the epipleurals to distinguish these two is not applicable because Orestias agassizii does not possess bifid epipleurals as described by him for O. pentlandii. Moreover, Crenichthys nevadae, a close relative of Empetrichthys, also has a few bifid epipleurals. Therefore, the only remaining character which could be cited to differentiate Empetrichthys from Orestias concerns the presence of parietals in the former and absence of these bones in the latter. However, a number of characters illustrate the differences between these two genera. These differences are listed in Table 9.

TABLE 9

OSTEOLOGICAL DIFFERENCES BETWEEN *EMPETRICHTHYS* AND *ORESTIAS*

Empetrichthys	*Orestias*
Parietals	
Present	Absent
Vomer	
Present	Absent
Preopercle	
Both vertical and horizontal portions of the preopercle elongated and pointed; a large bony lamina toward its anterior end and a sensory canal toward its posterior extremity; the shape is like other fundulids.	Both vertical and horizontal portions of the preopercle comparatively less elongated but rounded; a small bony lamina toward its anterior end and no sensory canal toward its posterior extremity; the shape is like *Rivulus* and other South American aplocheilids.
Postorbital	
Prominent as in *Fundulus* and other fundulids.	Very small as in *Rivulus* and other South American aplocheilids.
Anterolateral Processes of Lateral Ethmoids	
Small like other fundulids.	Long like South American aplocheilids.
Posterior Myodome	
Present	Absent

GROUP IV

Composition, Range and Habitat

The group consists of the monotypic genus Valencia. It is the only living genus of the Old World which superficially resembles Fundulus and is represented by Valencia hispanica (Cuvier and Valenciennes) from fresh waters of Spain. Fundulus letourneauxi (Sauvage), which has been mentioned in the literature as a second species of Valencia from Corfu, has been described by Myers (1938: 137) to belong to Aphanius.

Osteology

The skeletal characteristics of Valencia hispanica are very similar to those of Profundulus hildebrandi and to a lesser degree to those of Fundulus chrysotus. Because of these points of agreement the osteological description of the New World fundulids (Group III) is used as a basis in the following description of Valencia hispanica, but the account given for Cyprinodon generally applies to this species also.

The occipital region consists of the usual four occipital bones. The supraoccipital stops short of reaching the foramen magnum and consequently only the exoccipitals form the sides and the roof of the foramen magnum. Both the basioccipital and the exoccipital condyles are prominently developed and through them the skull articulates with the first vertebra. The neural arches of the first vertebra are separate from the occipital region of the skull.

The entire ethmoid region, including the mesethmoid composed of double ossified laminae, lateral ethmoids and a vomer, is much like that of Profundulus. The nasals are almost round and have their anterior extremities drawn forward to a noticeable degree.

The palatoquadrate bar of the mandibular arch has both quadrate and autopalatine ossifications. The entopterygoid is applied to quadrate and autopalatine bones from behind. The metapterygoid is absent.

Both the outer and inner processes of the maxilla are well developed. The mesial process of the maxilla is, however, more elongated than the New World fundulids. The premaxillary processes are broad and elongated.

In the lower jaw, articular, angular, sesamoid articular and dentary bones are present as in the other cyprinodonts.

Both the premaxilla and the dentary bear conical teeth. The outermost row of teeth is longer than the inner teeth which are arranged in a band.

The hyoid arch consists of the hyomandibular and the symplectic as in other cyprinodonts.

The hyoid cornu is normally disposed and consists of the usual bony elements. The hypohyal is represented by a single piece on each side.

Six branchiostegal rays are present on each side.

In the otic region, the pterotics slope gradually toward the lateral corners of the skull as in Produndulus but epiotic processes are lacking. As in other cyprinodonts, an opisthotic is absent.

There are distinct parietals in the orbitotemporal region of the skull and the supraorbital processes of the frontals are well developed. A wide notch is present between the posterior edge of the supraorbital process and the sphenotic process to accommodate the well-developed postorbital. Compared to Profundulus and other New World fundulids, the preorbital in Valencia hispanica is narrow but it is not as narrow as in the aplocheilids (Group V). In this connection it is appropriate to note that the preorbital is also narrower in Aphanius, Anatolichthys and Kosswigichthys than in the New World cyprinodontids related to Cyprinodon. The dorsolateral processes of the parasphenoid extend laterally to come in contact with the alisphenoids and thereby enclose a wide myodome as in Empetrichthys, Fundulus cingulatus and Fundulus kansae. An anteromesial process of the protoic is lacking and, therefore, this bone takes no share in the formation of the posterior myodome. As in other cyprinodonts, the basisphenoid is absent.

The branchial skeleton consists of five gill arches with the fifth one modified into the lower pharyngeals. There are twelve gillrakers in Valencia hispanica and most of them are shaped like a rosette. The third hypohyals bear a small patch of conical teeth and a similar but larger patch extends laterally along the fourth ceratobranchials up to half their length.

The basihyal and the urohyal are normally disposed and there are only two ossified basibranchials.

Four epibranchials are present as in other cyprinodonts. The first pharyngobranchial is cartilaginous but the other three are separate and bear conical teeth.

The lower pharyngeals are of normal shape and their anterior extremities come in close contact with the fourth ceratobranchials.

The posttemporal is unforked.

Summary of Significant Osteological Characters of Group IV

The summary of the osteological characters given for the New World fundulids (Group III) will apply equally to Valencia with the following modifications:

Otic Region

(1) No posteriorly directed otic processes.

Orbitotemporal Region

(2) Preorbital rather narrow in comparison to those of New World fundulids.

(3) Posterior myodome similar to Empetrichthys, Fundulus cingulatus and Fundulus kansae.

Other Characters

(4) Third and fourth pharyngobranchials separate as in Profundulus hildebrandi. In this respect both Valencia and Profundulus agree with aplocheilids and differ from other New World fundulids.

(5) Median hypural is divided into two equal parts by a median slit.

(6) Neural arches of the first vertebra separate from the occipital region and do not meet above the neural canal to form a neural spine. A bony septum, as in Profundulus, connects the neural arches a little below their distal extremities.

(7) Branchiostegals six.

Relationships of Valencia hispanica (Group IV)

Myers (1951: 249-250) indicated the close relationship of Valencia and the New World fundulids (Group III) by including both in the tribe Fundulini. Further, he (loc. cit.) commented on Valencia, which has a narrow preorbital: " . . . this genus may represent the ancestral stock from which the Rivulini have sprung." Kosswigichthys, due to its conical teeth, was thought to be related to Valencia and the New World fundulids. However, as has already been pointed out, experimental hybridization and cytological studies by Aksiray (1952) and Oztan (1954) demonstrate that Kosswigichthys actually is related to Aphanius and Anatolichthys. My study has produced osteological evidence in support of this latter conclusion. Hoedeman and Bronner (1951) erected the tribe Profundulidi to include Profundulus and and Adinia of New World and Valencia and Kosswigichthys of Old World, but Miller (1955: 10-11) regarded this arrangement as unnatural and suggested its abandonment. Steinitz (1951: 121) regarded Valencia as a relatively old and generalized type in contrast to the more recently evolved and highly specialized Kosswigichthys. Miller (1955: 11) wrote about Valencia: "An examination of specimens of Valencia hispanica and of syntypes of V. letourneuxi convinces me that this genus is a generalized, independent derivative probably not closely related to any New World genus."

Myers (1928) established the genus Valencia, formerly included in Fundulus to receive the only Old World Fundulus-like species Fundulus hispanica from Spain. As mentioned previously, another species Fundulus letourneauxi from Corfu, which is mentioned in the literature as a second species of Valencia, is according to Myers (1958) an Aphanius. Because Miller (1955) recently referred to this species as Valencia letourneauxi further study is needed to clarify its relationships.

Myers (1928) in describing Valencia, mentioned that the absence of a genital pouch was the only important diagnostic feature in which this genus differed from the New World fundulids. But the genital pouch is also absent in Empetrichthys and Crenichthys and is very weak in Profundulus.

My study shows that the osteology of Valencia hispanica is very similar to that of the New World fundulids. Except for the preorbital, which is comparatively narrow in Valencia, there are no osteological characters which are not found in the New World fundulids. It is pertinent to point out here that the preorbital is also narrow in

Empetrichthys and *Crenichthys*. In fact no osteological character has been found which would distinguish *Valencia* from the New World fundulids.

In spite of this close resemblance of *Valencia* to the New World fundulids, relative to both its osteological and other features, it has been suggested by Myers (1958) and by Miller (1955) that it is not phylogenetically close to the New World fundulids. *Valencia*, therefore, needs further study to clarify its correct relationships.

In the absence of any detailed morphological information about *Valencia* and *Profundulus*, both of which have been shown to be generalized primitive types, the only other information which might throw some light on their relationships is their exclusive occurrence in fresh water. Whether this has been always the case is not clear.

It is possible that some widespread ancestral stock structurally resembling the widely distributed aplocheilids of today entered the fresh waters of Central America and Spain to later produce *Profundulus* and *Valencia* respectively.

GROUP V

Composition, Range and Habitat

The group is almost world-wide in distribution and includes the largest number of species of oviparous cyprinodonts. Its members range throughout most of tropical America from Santo Domingo and southern Mexico to Columbia and La Plata, Ethiopian and Nile regions of Africa, Madagascar, the Seychelles and in Asia from Malabar to Siam on the mainland and southward to Borneo in the East Indes.

The following genera are included:

Tropical America

Rivulus Poey. Over thirty-seven species are known.

Range: Mexico, Central America, Antillean Islands, South America (from Colombia to La Plata). Harrington and Rivas (1958) have reported a species, Rivulus marmoratus from Florida (Indian River and Biscayne Bay).

Habitat: fresh, brackish and marine littoral waters.

Rachovia Myers. Two species.

Range: Colombia.

Habitat: ponds and mudholes which dry up once a year.

Pterolebias Garman. Two species.

Range: Orinoco River Basin, Venezuela; Santarem on the Lower Amazon, Brazil; and Peruvian Amazon.

Habitat: fresh water.

Cynolebias Steindachner.

Range: Eastern South America from Buenos Aires to northeastern Brazil.

Habitat: ponds and mudholes which dry up once a year.

Rivulichthys Myers. Monotypic.

Range: upper Paraguay and Amazonian tributaries of Matto Grosso in Brazil.

Habitat: fresh water.

Neofundulus Myers. Monotypic.

Range: reported from Aroyo Trementina, Paraguay and a clay pit on the east bank of the Rio Cuyaba at Pari, six km. from the town of Cuyaba, Matto Grosso, Brazil.

Habitat: fresh water.

Austrofundulus Myers. Three species.

Range: Venezuela.

Habitat: ponds and pools which dry up once a year.

Trigonectes Myers. Monotypic.

Range: reported from Porto Nacional, Rio Tocantins, Boyaz, Brazil.

Habitat: fresh water.

Hubbsichthys Schultz. Monotypic.

Range: reported from Pampan, Estado de Trujillo, Venezuela and possibly in Rio Motatan drainage.

Africa, Madagascar and the Seychelles

Aphyosemion Myers. About thirty-seven species.

Range: coastal region of West Africa (Liberia, Gold Coast, southern Nigeria, Cameroons, Gaboon and over the entire Congo Basin).

Habitat: fresh and brackish waters including pools and mudholes which dry up once a year.

Nothobranchius Peters. About thirteen species.

Range: Somaliland and Mozambique to the Central African Lakes and northern Nigeria. It is not found in the Congo Basin or the West African rain-forest where Aphyosemion occurs.

Habitat: fresh and brackish waters including pools and mudholes which dry up once a year.

Pachypanchax Myers. Three species (Myers, 1933: 182).

Range: Seychelles Islands and Madagascar.

Epiplatys Gill. More than twenty-five species.

Range: Africa except the eastern part.

Habitat: fresh and brackish waters.

Asia

Aplocheilus McClelland. About seven species.

Range: India, Burma, Malay Peninsula, Siam and Indo-Australian Archipelago.

Habitat: fresh, brackish and marine littoral waters.

Osteology

The account is based on a study of seven species representing six of the fourteen currently recognized genera comprising the group. Several genera (*Rivulichthys*, *Neofundulus*, *Hubbsichthys*), known only from one or two specimens and collected but once, need reinvestigation based on more representative material to establish their separate validity (Myers, 1927, 1942; Shultz, 1949). The species which have been studied are: *Rivulus bondi* Schultz, *Cynolebias whitei* Myers, *Austrofundulus stagnalis* Schultz, *Aphyosemion australe* (Rachow), *Aphyosemion caeruleum* (Boulenger), *Nothobranchius taenopygus* (Hilgendorf) and *Aplocheilus panchax* (Hamilton Buchanan).

The head skeleton of *Aplocheilus lineatus* has been described by Ramaswami (1946) and Kulkarni (1948). Their papers include pertinent details of the osteology of the genus *Aplocheilus*.

The osteological characteristics of the species studied are very similar and, therefore, the following description will apply equally to all of them.

In all the genera of Group V included in this study (Figs. 45, 46 and 49), the skull is characteristically flat and depressed. Moreover, the postorbital region of the skull, behind the laterally projecting sphenotic processes is very broad. The skull may be described under the usual four headings: the ethmoid region, the orbitotemporal region, the otic region and the occipital region.

Ethmoid region

The ethmoid region differs markedly from that of the cyprinodonts in Groups I, III, IV, VII and VIII, in that an ossified mesethmoid is absent. Instead, as in Groups II and VI (presently to be described), the mesethmoid in the members of Group V is a small, median heart-shaped cartilage, situated in the anterior depression of the ethmoid region. This cartilaginous mesethmoid is broad in front and narrow behind. The posterior extremities of the premaxillary processes rest on this cartilage and are closely attached to it by muscular tissue. The cartilaginous mesethmoid is also in close contact with the maxillae and the rostropalatine processes of the autopalatines of both the sides. The mesethmoid slides backward and forward with the movement of the premaxillary processes and, consequently, its attachment with adjacent bones helps to coordinate the movements of the jaws. A similar situation has been described in Aplocheilus lineatus by Kulkarni (1948). Except for Aplocheilus in which the anterolateral processes of the lateral ethmoids are small, all the other genera under consideration possess long and well-developed anterolateral processes. The vomer is a prominent median bone attached by its attenuated posterior end to the ventral surface of the parasphenoid. The mediolateral edges of the vomer are drawn out and come in contact with the lateral ethmoids from below. The anterior end of the vomer is pointed and provided with a patch of conical teeth (Figs. 46 and 49A). The paired nasals are small and irregularly shaped.

Orbitotemporal region

The orbitotemporal region is well developed and generally resembles that of Fundulus and its allies (Group III). The parietals, however, are variable in the genera under consideration (Group V). The parietals are absent in Nothobranchius; absent or fused with the posterior edges of the frontals in Austrofundulus, Aphyosemion; small in Cynolebias; and well developed in Rivulus and Aplocheilus. The frontals are well developed and extend considerably forward over the ethmoid region. The supraorbital processes of the frontals are extensive and cover the eyes completely. In the posterior orbital region, each supraorbital process of the frontal has a wide notch for the reception of the postorbital. In Aplocheilus the postorbital is a well-developed, boat-shaped bone with an open groove for the lateral line sensory canal toward its outer surface. The postorbital, however, is very small and inconspicuous in all the other genera under considerer-ation. The interorbital area of the frontals is rectangular. The lachrymal is characteristically twisted with its upper and smaller portion directed anteriorly and horizontally while its lower, comparatively longer limb is vertically disposed. A vertical median groove runs the entire length of the lachrymal. This is termed an aplocheilid type of lachrymal which is characteristic of Group V. The parasphenoid is prominently located on the ventral side of the skull. It is, in comparison to that of other cyprinodonts, a wide bone and extends considerably forward in the ethmoid region. Except in Rivulus where the anterolateral processes of the parasphenoid extend laterally to meet the alisphenoids and thereby enclose posterior myodomes on both sides, the anterolateral processes in all the other genera are small and do not meet the alisphenoids. Consequently, posterior myodomes are absent in all these genera.

Otic region

The otic region is similar to that of other cyprinodonts except that the laterally projecting sphenotic processes are broader at their extremities. The epiotic processes and the opisthotics are absent.

Occipital region

The occipital region is composed of the usual four bones, the supraoccipital, the basioccipital and the two exoccipitals. The exoccipitals complete the roof and the side walls of the foramen magnum while the floor of the latter structure is formed by the basioccipital. The supraoccipital stops short of reaching the foramen magnum and, therefore, takes no part in its formation. Both the basioccipital and the exoccipitals bear prominent condyles for articulation with the first vertebra. The neural arches of the first vertebra are separate from the occipital region and take no part in the articulation. The first vertebra has a distinct neural spine and also possesses corresponding facets towards its anterior end for articulation with the skull.

Visceral skeleton

The palatoquadrate bar of the mandibular arch in these six genera of cyprinodonts is unique in possessing an additional bony element, the metapterygoid (Figs. 47A, 50A, and 57A). Starks (1904), Regan (1911), and Myers (1951), in listing the distinguishing characters of the suborder Poecilioidea of the family Cyrpinodontidae stated that the metapterygoid is absent in the group. However, the metapterygoid is present in its normal position in each of the seven species examined in this study (Rivulus bondi, Cynolebias whitei, Austrofundulus stagnalis, Aphyosemion australe, Aphyosemion caeruleum, Nothobranchius taeniopygus and Aplocheilus panchax). It is well ossified and its relationship with the hyomandibular, symplectic, quadrate and mesopterygoid confirms its identity. Moreover, it agrees in its position and shape with a similar bone in the Haplomous fish Novumbra hubbsi (Chapman, 1934). Similarly Ramaswami (1946)and Kulkarni (1948) found this bone in Aplocheilus lineatus. Kulkarni (op. cit.) also mentioned its presence in one additional species, Aplocheilus blochii (A. parvus of Sundra Raj, 1916) and A. panchax, a species which is included in this study. Kulkarni (op. cit.), therefore, pointed out the necessity for a revision of the present distinguishing characters of the suborder Poecilioidea. The presence of a distinct metapterygoid in so many different genera, as revealed in this study, confirms the need for such a reappraisal. The metapterygoid in all these species lies above the symplectic with which it is closely associated; posteriorly it extends underneath the membranous portion of the hyomandibular; anteriorly it comes in contact with the mesopterygoid and the quadrate. Except for Cynolebias in which this bone is splint-like, it is quite prominent in all the other genera.

The symplectic is large and prominent. The hyomandibular, the quadrate, the autopalatine and the mesopterygoid are normally disposed. The rostropalatine process of the autopalatine is long, extends forward, and is well separated from the ethmopalatine process of the same bone.

The premaxillae bear small but uniformly broad premaxillary processes which extend to the dorsal surface of the cartilaginous mesethmoid (Figs. 48C and 51C).

The maxillae are similar to those in Fundulus and its allies (Group III). The much elongated mesial processes of the maxillae are disposed horizontally instead of more or less anteriorly as in Fundulus and its allied (Fig. 50B). Each premaxilla is provided with conical teeth arranged in a band.

The mandibular bar of the palatoquadrate arch is like that of other cyprinodonts in number and arrangements of its bony elements and the dentaries bear teeth similar to the premaxillaries.

The usual four opercular bones are present but the preopercle is of normal shape only in Aplocheilus. In the other genera under consideration it differs in that both the upper vertical and the lower horizontal portions are broad. This broadness is particularly pronounced in the lower portion which fails to extend forward under the quadrate in the customary manner. Moreover, in all the genera except *Aplocheilus*, the membranous expansion between the two limbs of the preopercle is less extensive than is usual in cyprinodonts.

Branchial arches (Fig. 48B)

There are five branchial arches and each is composed of two lateral halves containing the same number of bony elements as in other cyprinodonts. There are, however, three ossified basibranchials similar to those of *Oryzias* (Group VII). This is in contrast to only two of these elements in all the other cyprinodonts included in this study. The additional piece lies immediately posterior to the basihyal and is smaller than the other two basibranchials. Except for *Oryzias latipes*, such an ossified basibranchial is not present in the other cyprinodonts examined during the course of this study. In these latter cyprinodonts the first and the fourth basibranchials remain unossified while in the group under discussion and *Oryzias* (Group VII) only the fourth basibranchial is unossified and there are three ossified basibranchials. Three ossified and the fourth unossified basibranchials have also been described in *Aplocheilus lineatus* and *Oryzias melastigma* by Kulkarni (1948).

The epibranchials, pharyngobranchials and ceratobranchials are normally disposed. Unlike other cyprinodonts, except *Profundulus* and *Valencia*, the third and fourth pharyngobranchials are separate and do not fuse to form a single plate.

Hyoid arch

The dorsal portion of the hyoid arch includes the hyomandibular and the symplectic. The hyomandibular has a quadrilateral shape in contrast to the elongate one normal to other cyprinodonts.

The hyoid cornu is similar to that of other cyprinodonts except for the hypohyals which are represented by two pieces on both sides. There are six branchiostegals in all the seven species included in the present study. The branchiostegals are arranged in two groups--the first contains two rays and the second has four. Two of the outermost rays are broader than the others. The basihyal and the urohyal are normally disposed.

In Aplocheilus the posttemporal is unforked; in Austrofundulus, Cynolebias, and Nothobranchius, it is unforked, but towards its base a portion of the ligament connecting it to the exoccipital may be ossified; in Rivulus and Aphyosemion (both species) it appears to be forked because the ligament to the exoccipital is ossified for about half its length (Figs. 48A, 51B, 56D and 57B).

Summary of Significant Osteological Characters of Group V

Ethmoid Region

(1) Mesethmoid cartilaginous.

(2) Vomer dentigerous.

Orbitotemporal Region

(3) Parietals variable: well developed in Rivulus bondi, Aplocheilus panchax, Aplocheilus lineatus (Kulkarni, 1948); small in Cynolebias whitei; inconspicuous in Austrofundulus stagnalis, Aphyosemion australe, Aphyosemion caeruleum; and absent in Nothobranchius taeniopygus.

(4) Anterolateral processes of the parasphenoid variable: in Rivulus they are long and extend laterally to meet alisphenoids and thereby enclose posterior myodomes on either side; in all other forms studied, no posterior myodome is formed because these processes do not meet the alisphenoids.

(5) Interorbital area rectangular; supraorbital processes of the frontals well developed and cover the eyes completely.

(6) Foramen magnum formed by the basioccipital and exoccipitals; supraoccipital stops short of reaching the foramen and therefore takes no part in its formation.

(7) Both the basioccipital and exoccipitals bear condyles for articuation with the first vertebra.

(8) The transverse processes of the first vertebra meet dorsally to form a distinct neural spine and take no part in the articulation.

Otic Region

(9) No epiotic processes.

Visceral Skeleton

(10) Metapterygoid present.

(11) Teeth conical and arranged in a band.

(12) Premaxillary processes small, uniformly broad and extending over the mesial processes of the maxillae to come in contact with the mesethmoid cartilage.

(13) Upper portion of the maxilla with well-developed mesial and less well-developed outer processes.

(14) Hypohyals on each side represented by two bony pieces.

(15) Six branchiostegals arranged in two groups--first group with two rays and the second group with four.

(16) Third and fourth pharyngobranchials separate.

(17) Three basibranchials.

Other Regions

(18) Posttemporal slightly forked to unforked: forked to half its extent in Rivulus bondi and Aphyosemion (both species); unforked but with a portion of the ligament connecting it to the exoccipital ossified towards the base in

Austrofundulus, *Cynolebias* and *Nothobranchius*; distinctly unforked in *Aplocheilus*.

(19) Transverse processes of the precaudal vertebrae elongate.

(20) Subcleithral bone present in *Rivulus*, *Austrofundulus* and *Cynolebias* (New World aplocheilids); absent in *Aphyosemion* (both species) and *Aplocheilus*.

(21) Wide haemal canals in *Aplocheilus*; not so wide in the other genera.

(22) Prezygapophyses prominent and meet dorsally to enclose canals.

(23) Hypural trifid in *Aplocheilus* *panchax*, bifid in the other species (Fig. 58).

Relationships of Group V

These widely separated genera of cyprinodonts agree rather closely in their osteological characters. All of them possess a metapterygoid, three ossified basibranchials, an enlarged dentigerous vomer, a hypohyal on each side represented by two bony pieces, separate third and fourth pharyngobranchials, prominent prezygapophyses which meet dorsally to enclose canals, and a bifid or trifid hypural. On the basis of these characteristics, the group appears to be a well-defined assemblage of genera despite the variation noted relative to the posttemporals and the parietals. Taken collectively, these characteristics, including those which show variation, indicate that the aplocheilids are more generalized than any other taxon in the order cyprinodontiformes. The skeletal elements of aplocheilids appear to form a foundation material which, by either loss or modification, has evolved into characteristics of the other groups within this order. The present high degree of diversity within the aplocheilids, however, suggests an ancient lineage and the possibility that a once widespread ancestral stock similar to them produced not only the aplocheilids but also other groups as well.

In the possession of a metapterygoid this group shows agreement with the family Amblyopsidae, suborder Amblyopsoidea. Hitherto, following Regan (1911), it has been supposed that the metapterygoid was absent in the suborder Poecilioidea to which all the cyprinodonts except amblyopsids belong. It is entirely possible that the amblyopsids, as well as other groups of cyprinodonts evolved from aplochilid-like ancestors, when the latter were more widespread. The present distribution of the amblyopsids, restricted as they are to the swamps, caves and springs of the southeastern and central United States lends additional support to this view (Woods and Inger, 1957).

The Aplocheilids show relationships with both the peculiarly organized genus *Orestias*, from the high Andes of Peru, and the fundulids of North America. They seem to be related to *Orestias* in the possession of lateral ethmoids with well-developed anterolateral processes, prominent prezygapophyses meeting dorsally to enclose canals, small postorbital, pharyngeal teeth with a slight shoulder as in *Rivulus* and the shape of the preopercle which in *Orestias* is more like that of the South American aplocheilids. The details of this relationship are discussed in connection with the genus *Orestias*.

In the possession of the parietals, the exoccipital condyles, the formation of the foramen magnum by the basioccipital and exoccipitals, the nature of the upper portion of the maxilla, and the nature of the transverse processes, the aplocheilids seem to be related to the fundulids. They are more closely related to *Profundulus*, *Empetrichthys* and *Crenichthys* in certain other characters which have already been described in connection with the three latter genera.

The aplocheilids show relationships to the aphanids as well as aplocheilichthyians (including *Lamprichthys*) in possessing a cartilaginous mesethmoid, the nature of the occipital region with well-developed exoccipital condyles. They, however, seem to be more closely related to the plocheilid thyians in the nature of the premaxillary processes, elongated transverse processes, prominent prezygapophyses meeting dorsally to enclose canals and the close similarity of the pectoral girdles of Aplocheilus and the plocheilichthyians.

The aplocheilids are related to Valencia in the same characters as they are to the North American fundulids.

The aplocheilids also show affinity with the peculiar Asiatic genus Oryzias in possessing well-developed exoccipital condyles, in the nature of the premaxillary processes, in the twisted and narrow character of the preorbital, in possessing three ossified basibranchials, in the bifid hypural and in the close resemblance between the pectoral girdles of Aplocheilus and Oryzias.

It seems probable that the aplocheilids gave rise to all those groups with which they show relationship. The restricted distribution of the groups which were derived from the aplocheilids in different parts of the world and the world-wide distribution of the aplocheilids seem to support this conclusion. Moreover, as has already been pointed out, they possess certain generalized characters which were either dropped or modified in the other groups. The aplocheilids, therefore, may well be considered a basic group from which various other groups of cyprinodonts have evolved.

GROUP VI

Composition and Range

The members of this group are confined to the Ethiopian and the Nile regions of Africa. The following genera are included:

Procatopus Boulenger. Four species.

Range: confined to the Cameroons.

Hypsopanchax Myers. Three species.

Range: confined to Central Africa (the Congo, the Ogowe river systems and the Lake Edward area.)

Platypanchax Ahl. Monotypic. Differs from *Hypsopanchax* only in dentition.

Aplocheilichthys Bleeker. Thirty-eight described forms, some are perhaps not valid and many good species still remain undiscovered (Myers, 1938: 142).

Range: from Nile and Guinea south to Angola and Zululand.

Micropanchax Myers. For certain species of *Aplocheilichthys*. Later amalgamated by Myers (1938) with *Aplocheilichthys*, but again revived by Schultz (1942). E. Trewavas, of the British Museum, also considers it to be a valid genus (personal communication).

Cynopanchax Ahl. Monotypic.

Range: Bukoba, N.W. Tanganyika Territory.

Plataplocheilus Ahl. Monotypic.

Range: "Attogondema, Nga R., Cameroon." (Myers, 1938: 143).

Lamprichthys Regan. Monotypic.

Range: Lake Tanganyika.

Osteology (Figs. 54 and 55)

This account is based on a study of four species representing two of the seven genera comprising the group. The three genera described by Ahl (1928) mainly on the basis of teeth may not be tenable on further study as has been pointed out by Myers (1938b). The species which have been studied are:

Aplocheilichthys johnstonii (Gunther), *A. katangae* (Boulenger), *Micropanchax loati* (Boulenger), and *M. schoelleri* (Boulenger).

The osteological characteristics of these four species are very similar and, therefore, the following description will apply equally well to all of them. In all the four species the skull is flat and uniformly broad behind the postorbital and the orbital regions.

The ethmoid region consists of the nasals which are roughly triangular in shape and almost round on their posterior edges. The lateral ethmoids are prominent but the vomer is small and without teeth. The mesethmoid is cartilaginous.

The orbitotemporal region lacks parietals on the dorsal side. The frontals are well developed and their supraorbital processes are extensive. There is a wide notch behind the supraorbital process and the sphenotic bone. Both the postorbital and the lachrymal are well developed. The parasphenoid is normally located on the ventral side. The inner processes of the parasphenoid are small and fail to meet the alisphenoids and, consequently, the posterior myodome is absent.

The otic bones are located as in other cyprinodonts and the opisthotic is absent. A prominent cartilaginous area is present on both sides between the otic bones and the frontal.

The occipital region consists of the usual four occipital bones. The exoccipitals bear prominent exoccipital condyles and form the sides and roof of the foramen magnum. The supraoccipital stops short of reaching the latter structure. The basioccipital bears a prominent basioccipital condyle and is located on the ventral side of the skull.

The palatoquadrate bar of the mandibular arch shows two ossifications, the quadrate and the autopalatine. The metapterygoid is absent. The mesopterygoid is applied to the quadrate and the autopalatine from behind.

The mandibular portion of the mandibular arch contains an articular bone in the lower jaw and a small piece of the Meckel's cartilage which persists in the adults. The dentary and the angular are present in their normal positions.

The upper jaw consists of paired maxillae and the premaxillae. The premaxillary processes are broad as in aplocheilids. These processes are close together and are connected to the cartilaginous mesethmoid. In Micropanchax loati, both the outer and the mesial processes of the maxilla are well developed but in the other three species the outer process of the maxilla is better developed than the mesial process. The maxillas are edentulous while both the premaxillas and the dentaries are provided with variable rows of conical teeth. The outermost row in all of them consists of comparatively larger teeth. There are four rows of teeth in Aplocheilichthys katangae, three rows in A. johnstonii and Micropanchax schoelleri, and two rows in M. loati.

The hyomandibular, the symplectic and the hyoid cornu are located in their normal position. The hypohyal on each side is represented by a single piece and both the urchyal and the basihyal are normally positioned.

In both species of Aplocheilichthys under discussion, there are five branchiostegal rays--the first group has one ray and the second group has four. In the two species of Micropanchax there are, however, four branchiostegal rays--none in the first group and four in the second.

The branchial skeleton is similar to that of other cyprinodonts. There are five gill-arches consisting of the usual segments and showing similar modifications. The four epibranchials are similar in structure. The first pharyngobranchial is cartilaginous, the second is a separate ossified piece with conical teeth, the third and the fourth are fused to form a single ossified plate with conical teeth.

There are nine gill-rakers in Micropanchax loati, ten in M. schoelleri, and eight in Aplocheilichthys katangae. The gill-rakers were not counted in A. johnstonii.

The opercle bones are normal in all four species.

The posttemporal is unforked and there are two ossified basibranchials.

Summary of Significant Osteological Characters of Group VI

Ethmoid Region

(1) Mesethmoid cartilaginous.

(2) Vomer edentulous.

Orbitotemporal Region

(3) Parietals absent.

(4) Posterior myodome absent.

(5) Anterolateral processes of the parasphenoid small and not meeting the alisphenoids.

(6) Postorbital and preorbital (lachrymal) well developed.

Occipital Region

(7) Foramen magnum formed by the basioccipital and exoccipitals.

(8) Supraoccipital not reaching foramen magnum and, therefore, does not share in its formation.

(9) Both the basioccipital and exoccipital condyles well developed.

(10) Articulation between the skull and first vertebra through the condyles.

(11) First vertebra with distinct neural spine; neural arches separate from the occipital region.

Visceral Skeleton

(12) Metapterygoid absent.

(13) Teeth conical and arranged in two to four rows in the species under consideration.

(14) Premaxillary processes small and broad.

(15) In Micropanchax loati, both mesial and outer processes of upper portion of maxilla well developed; in the other three species only the outer processes of the maxillae well developed.

(16) Hypohyal on each side represented by a single piece.

(17) Branchiostegals five in Aplocheilichthys and four in Micropanchax.

(18) Third and fourth pharyngobranchials fused.

(19) Two ossified basibranchials.

Other Regions

(20) Posttemporal unforked.

(21) Transverse processes of precaudal vertebrae elongated.

(22) Prezygapophyses elongated and joined dorsally to enclose canals.

(23) Pelvic fin rays elongated.

(24) Space between the coracoid and the cliethrum of pectoral girdle very prominent.

(25) Pectoral fins high set.

(26) Median hypural a single fan-shaped piece.

Relationships of Group VI

The genera comprising Group VI form a closely interrelated and homogeneous unit. Their chief diagnostic feature relates to the high position of the pectorals; the upper ends of the bases of these fins are located above the midline of the body. This character alone sets them apart from other African cyprinodonts except for *Lamprichthys tanganicanus*. This species approaches the aplocheilichthyians in the position of the pectorals and is similar to them in many other osteological characters. Therefore, *Lamprichthys tanganicanus*, should not be separated from the members of Group VI as has been done in the past.

Myers (1931: 11) erected a separate subfamily for the sole reception of *Lamprichthys tanganicanus*, although he realized that in this species "The pectoral fins are set high, possibly indicating relationship to the Aplocheilichthyini." The osteological characters mentioned by him for the subfamily Lamprichthyini are untenable on the basis of this study. Contrary to his description, both the basisphenoid and the parietals are absent in *Lamprichthys tanganicanus*.

Again, while describing the osteological and other characters of the subfamily Lamprichthyini Myers (1936) listed additional characters which he thought were peculiar to this subfamily. These characters are: numerous vertebrae, ctenoid scales, closely scaled lunate caudal fin, connected pelvic fins inserted very nearly under the pectorals, anal fin very long, compressed atherinid-like form and silvery color.

Many of the above mentioned characters are also shared by aplocheilichthyians. For example, the number of vertebrae in *Procatopus* is numerous, 29 or 30 (Myers, 1938: 140), although not as numerous as in *Lamprichthys tanganicanus* which has 41 vertebrae (Myers, 1931: 11, and my own count). The caudal fin, although subtruncate in *Procatopus nototaenia* Boulenger (one specimen examined through the courtesy of Dr. James Bohlke, ANSP 66852), is scaled almost to the same extent as in *Lamprichthys tanganicanus*. Moreover, in *P. nototaenia* as in *L. tanganicanus*, the pelvic fins are long, pointed, their bases contiguous and connected by a membrane, and they are distinctly situated under the pectoral base. The anal fin is long in *Procatopus* and has 13 to 17 rays; in *Hypsopanchax* the number of anal rays is 14 to 21 (Myers, 1938: 140). The body is compressed in almost all the members of aplocheilichthyians but it is strongly compressed in *Cynopanchax*, *Procatopus*, *Platypanchax* and *Hypsopanchax* (Myers, *loc. cit.*). About *Hypsopanchax* Myers (*loc. cit.*) wrote: "The very compressed body, the deep, flattened and sharp abdominal edge, and the shallow caudal peduncle distinguish this peculiar genus from *Aplocheilichthys*."

Thus it is difficult to justify the erection of a separate subfamily for the sole reception of *Lamprichthys tanganicanus* chiefly on the basis of its ctenoid scales and its numerous vertebrae, for such a treatment ignores the overwhelming similarities which this species seems to share with such aplocheilichthyians as *Procatopus*, *Hypsopanchax*, and *Platypanchax*, which should not be separated from it. Moreover, the osteological characteristics of aplocheilichthyians which have been included in this study and *Lamprichthys tanganicanus* are so similar as to offset the differences in the number of vertebrae and the nature of the scales.

Another point of agreement between *Procatopus* and *Lamprichthys* which Myers (1936 and 1938) also described but whose significance he apparently failed to appreciate is the similarity of the nature of their haemal arches. Four of the haemal arches in *Procatopus* (Myers, 1938) and 12 in *Lamprichthys tanganicanus* (my observations) are expanded for the reception of the posterior end of the large air-bladder.

The various genera of aplocheilichthyians have been delimited into two groups by Myers (1938: 139) chiefly on the basis of differences in the branchiostegal rays and the position of the pelvic fins. These two groups are differentiated thus:

"1a. One or two of the branchiostegal rays of each side detached from the rest and projecting backward some distance from beneath the lower part of the opercle as a pointed process; pelvic fins placed anteriorly, under or almost under the base of the pectoral fins; . . . 1. Procatopus Boulenger.

1b. None of the branchiostegal rays detached and projecting backward from beneath the opercle; origin of pelvic fins behind the base of the pectorals. . . ." All the remaining genera are listed under this group.

The single branchiostegal ray of first group, on each side, is also detached in *Lamprichthys tanganicanus* and projects backward beneath the opercle, thus indicating close relationship of this species with *Procatopus*.

Therefore, because of the close relationship of aplocheilichthyians and *Lamprichthys tanganicanus*, I am suggesting that a single family Aplocheilichyidae be recognized to include not only all the genera currently placed in the tribe Aplocheilichthyini (Myers, 1951) but also the genus *Lamprichthys*. The chief diagnostic characters of the family Aplocheilichthyidae would be: high set pectoral fins, upper end of the fin base above the midline of the depth of the body at that point; wide preorbital, usually half the eye diameter or more; body rather deep and compressed; dorsal fin origin behind that of anal in all currently known forms; metapterygoid, vomerine teeth and pseudobranchiae absent.

The aplocheilichthyians and *Lamprichthys tanganicanus* show relationship to the widely distributed aplocheilids in the following characters:

(1) Cartilaginous mesethmoid.

(2) Foramen magnum formed by the basioccipital and exoccipitals.

(3) Supraoccipital stops short of reaching the foramen magmum and, therefore, takes no part in its formation.

(4) Both basioccipital and exoccipital condyles well developed.

(5) First vertebra with a distinct neural spine and with facets for the exoccipital condyles.

(6) Prezygapophyses prominent and joined to enclose canals.

(7) Close resemblance of the pectoral girdles in Aplocheilus and such genera as Aplocheilichthys, Micropanchax and Lamprichthys. The pectoral girdle in all of them has a large space between the coracoid and the cleithrum.

(8) Skull flat and depressed.

The aplocheilichthyians also show agreement with the aphanids (Group II) in possessing characters one through four, but these similarities may be due to parallel evolution rather than to any phyletic relationship.

The family Aplocheilichthyidae may be divided into two subfamilies:

1. Aplocheilichthyinae (new subfamily): Body not excessively deep and the abdomen not sharply compressed; pelvic fins usually inserted more posteriorly; none of the branchiostegal rays detached.

Genera: Aplocheilichthys, Cynopanchax,
Plataplocheilus, Micropanchax.

2. Procatopinae (new subfamily): Body deep, abdomen compressed; pelvic fins placed anteriorly under or almost under the pectoral base; one or two branchiostegal rays detached and projecting backward.

Genera: Procatopus, Lamprichthys,
Hypsopanchax, Platypanchax.

Relationships and Taxonomy of Lamprichthys tanganicanus

The relationships of Lamprichthys tanganicanus have been commented upon in connection with a similar question in aplocheilichthyians (Group VI). However, it seems appropriate that these relationships should be considered separately because the osteological characters of this species have been confused in the past and because an understanding of its taxonomy and precise relationships have suffered accordingly.

This monotypic genus appears to be confined to Lake Tanganyika in Africa. Myers (1931) established a separate subfamily for its reception. In doing this he relied chiefly on the observations of Regan (1911) for osteological characters of the species and assumed that, since Regan had included the species in the subfamily Fundulinae, the parietals were present and the epipleurals simple. Similarly Myers incorporated Regan's statement that the basisphenoid was present.

Later, while studying Lamprichthys tanganicanus in more detail, Myers (1936) listed the osteological characters of the species. This time, however, he did not make any comment about the parietals, but again stated that the basisphenoid was present.

I have prepared a skeleton of one specimen of this species and find that the parietals are absent. Further, as in all the other cyprinodonts which I have included in this study, the basisphenoid is absent. I am, however, in complete agreement with Myers' (1931: 11) comment that in the members of the subfamily Lamprichthyinae "The pectoral fins are set high, possibly indicating relationship to the Aplocheilichthyini."

In connection with the discussion of the relationships of Group VI, I have pointed out that there is a sufficient agreement between *Lamprichthys* and aplocheilichthyians, especially *Procatopus*, to justify the suggestion that two subfamilies be erected within one family, Aplocheilichthyidae, to show this relationship.

Moreover, the osteology of *Lamprichthys tanganicanus* is very similar to that of the aplocheilichthyians included in this study. The account given for them will apply equally to this species except for the greater number of vertebrae and the presence of more numerous (12) expanded haemal arches in *Lamprichthys tanganicanus* but, as has been pointed out previously, the haemal arches are also expanded in *Procatopus*.

Lamprichthys tanganicanus seems to be a modified descendent of an aplocheilichthys-like ancestor which might have gained access into Lake Tanganyika when it was formed in the Rift Valley during the Pliocene (Myers, 1936). The specializations present in *Lamprichthys tanganicanus* are adaptations to the vast and deep habitat of the lake. In this connection the following remarks of Myers (1936: 4) seem pertinent: "The peculiar athernid-like habitus and color of this fish sets it off as one of the most interesting specializations of the cyprinodonts. Evidently these little fishes have the same habits in the sea-like expanse of Tanganyika as have the atherines in the ocean."

GROUP VII

Composition and Range

This group contains a single genus Oryzias Jordan and Snyder and its species range from Japan and Central China southward to Celebes, Timor, Java and westward to Southern India. The chief character of these fishes concerns premaxillary which is non-protractile only in this group of cyprinodonts.

Osteology

The account which follows is based on Oryzias latipes (Temminck and Schlegel).

The head skeleton of Oryzias melastigma (McClelland) has been the subject of study by Ramaswami (1946) and Kulkarni (1948). Because the head skeleton of Oryzias latipes agrees sufficiently with that of O. melastigma, only those osteological characters which are of significance in the phylogenetic relationships of the genus will be emphasized in the following description. For the details of the head skeleton the descriptions of Ramswami (op. cit.) and Kulkarni (op. cit.) should be consulted.

In comparison with Aplocheilus lineatus (and other aplocheilids) the skull of Oryzias latipes is neither as flat nor as wide. It is slightly rounded posteriorly from where it gradually tapers toward the small jaws. The pterotics are situated at a lower level than the epiotics and the frontals.

The ethmoid region lacks a vomer. Instead the parasphenoid extends considerably forward to support the mesethmoid from below. The mesethmoid is composed of double ossified laminae. The lateral ethmoids are located normally but they are small bones in comparison to similar bones of the aplocheilids. The nasals are rectangular and are situated in their normal position.

In the orbitotemporal region the parietals are absent but the frontals are well developed and the supraorbital processes of the frontals cover the eyes completely. The interorbital area of the frontals is rectangular as in aplocheilids. The parasphenoid is rather narrow but its anterolateral processes are well developed and extend laterally to meet the anteromesial processes of the prootics to enclose posterior myodomes on both sides. The alisphenoids are located normally but they are not in contact with anterolateral processes of the parasphenoids and, therefore, take no share in the formation of the posterior myodomes. The boat-shaped postorbital is located outside and behind the sphenotic and takes no share in the formation of the postorbital wall of the cranium. The postorbital is provided with an open groove for the lateral line sensory canal. The lachrymal is characteristically twisted as in aplocheilids and a vertical groove runs its entire length.

The otic bones are normally located except for the sphenotics which are, in comparison to aplocheilids, more anteriorly placed and come in intimate contact with the posterior extremities of the supraorbital processes of the frontals, thereby obliterating the notch for the postorbital on both sides. The epiotics are provided with slender epiotic processes which are pointed at their tips.

The occipital region consists of the usual four bones, the supraoccipital, the basioccipital and the exoccipitals. The foramen magnum is formed by the basioccipital and the exoccipitals. The supraoccipital stops short of reaching the foramen magnum and, therefore, takes no part in its formation. The basioccipital is arched below and bears a median ridge ventrally. Both the basioccipital and the exoccipitals are provided with condyles for articulation with the first vertebra. The first vertebra bears corresponding facets for the exoccipital condyles and also has a distinct neural spine.

The palatoquadrate bar of the mandibular arch shows only two ossifications, the quadrate and the autopalatine, and to these the mesopterygoid is attached from behind. The metapterygoid is absent.

The upper and lower jaws, although containing the same bony elements as in other cyprinodonts, included in this study, have a distinctive organization.

In the lower jaw, a dentary, articular, angular and sesamoid articular are located in their normal positions. In the upper jaw the premaxillae are normally located and the premaxillary processes are short and broad as in aplocheilids. The premaxillary processes of the two sides are very close together and pass over the mesial processes of the maxillae to come in contact with the ossified mesethmoid.

The maxilla is modified differently than in any of the other cyprinodonts included in this study. The mesial process of the maxilla is elongate, very prominent, and runs under the premaxillary process of its side to lie in intimate contact with it. The upper portion of the descending limb of the maxilla has an anterior membranous expansion which overlaps the outer edge of the premaxilla. The autopalatine has a bifid rostropalatine process which encloses between its extremities a portion of the descending limb of the maxilla.

The arrangement and relationships of the premaxillae, maxillae and the rostropalatine processes of the autopalatines is such that the premaxillae fail to form protrusible jaws. The ethmopalatine process of the autopalatine is absent.

The premaxillae and the dentary bear conical teeth but there is some sexual dimorphism in the number and the nature of the teeth. The teeth are fewer in the males and, on both the dentary and the premaxillary, they are arranged in two rows. The teeth in the outer row, especially at the angle of the mouth, are considerably larger than those of the inner row. In the females, however, teeth are more numerous on both the dentary and the premaxilla. These teeth are arranged in a band and all of them are small and conical. Such sexual dimorphism of teeth also has been described by Sundra Raj (1916) and Kulkarni (1948) for Oryzias melastigma.

The opercle bones are disposed as in the other cyprinodonts. There are, however, some modifications in their shape. The opercle is quadrilateral in shape, but otherwise it is normally located. The subopercle does not differ from that of other cyprinodonts. The interopercle is broad posteriorly and considerably elongated anteriorly, for about two-thirds its length. The preopercle and especially its horizontal portion is comparatively small. The preopercle, moreover, extends only for a short distance below the symplectic and does not reach the quadrate bone.

As in *Oryzias melastigma* described by Kulkarni (1948), the interhyal is also absent in *Oryzias latipes*. The epihyal, the ceratohyal and the hypohyal are normally disposed. Kulkarni (*op. cit.*), however, reported the absence of hypohyals in *Oryzias melastigma*, but in *Oryzias latipes* the hypohyal on each side is present and represented by a single bony piece.

Both the basihyal and the urohyal are normally disposed and are similar to *Oryzias melastigma* as described by Kulkarni (1948).

There are five branchiostegals arranged in two groups as in other cyprinodonts. The first group contains one ray while the second group consists of four branchiostegals on each side.

The branchial skeleton consists of five branchial arches; the first four bear gill filaments and are normally disposed. The fifth arch is modified into lower pharyngeals similar to those of *Oryzias melastigma* as described by Kulkarni (1948), but differs considerably from other cyprinodonts in the shape of the lower pharyngeals (Fig. 56A).

Except for the second epibranchial which is small and nodular, the other three epibranchials are similar to other cyprinodonts described so far.

The first pharyngobranchial is cartilaginous, the second is a small ossified piece provided with conical teeth, but the third and the fourth are fused into a single well-developed plate. The latter bears towards its ventral surface about fourteen rows of small conical teeth.

There are three basibranchials, as in aplocheilids, and fifteen gill-rakers attached to the anterior surface of the first ceratobranchial.

Summary of Significant Osteological Characters of Group VII

Ethmoid Region

(1) Mesethmoid ossified composed of double laminae.

(2) Vomer absent.

Orbitotemporal Region

(3) Parietals absent.

(4) Posterior myodome formed by the union of dorsolateral processes of the parasphenoid and the anteromesial processes of the prootic; alisphenoid takes no part in its formation.

(5) Interorbital area of the frontals rectangular; supraorbital processes of the frontals less developed in comparison to Fundulus and aplocheilids.

(6) Sphenotics are anteriorly placed and come in contact with the posterior portions of the supraorbital processes of the frontals, thereby obliterating the notch for the postorbital on both sides.

(7) Postorbital is small and boat-shaped.

(8) Foramen magnum formed by the basioccipital and the exoccipitals; supraoccipital stops short of reaching the foramen and therefore takes no part in its formation.

(9) Basioccipital and exoccipital condyles well developed.

(10) Neural arches of first vertebra separate from the occipital region; no gap between first and second vertebrae.

(11) First vertebra with a distinct neural spine.

Otic Region

(12) Epiotic processes present.

Visceral Skeleton

(13) Metapterygoid absent.

(14) Teeth conical, show sexual dimorphism.

(15) Premaxillary processes short and broad.

(16) Upper portion of the maxilla expanded and supports a similar expansion of the premaxilla from below, thereby making the premaxilla nonprotractile. Maxilla with a well-developed mesial process and less-developed outer process.

(17) Autopalatine with two well-developed processes toward its upper end. These processes form a notch into which the maxilla is lodged and thus adding to the nonprotrusibility of the jaws.

(18) Lachrymal characteristically twisted and narrow (aplocheilid-like).

(19) Hypohyal on each side is represented by a single bony piece.

(20) Branchiostegals five, arranged in two groups; first group with one ray while the second group consists of four rays.

(21) Third and fourth pharyngobranchials fused to form a large upper pharyngeal plate with numerous rows of small conical teeth.

(22) Three basibranchials.

Other Regions

(23) Posttemporal unforked (Fig. 56B).

(24) No supracleithrum.

(25) Transverse processes of the precaudal vertebrae elongated.

(26) Haemal canals wide.

(27) Hypural bifid (Fig. 59).

(28) Pelvic girdle with an external lateral process (Fig. 56C).

(29) A large space between cleithrum and coracoid (Fig. 56B).

(30) No interhyal.

(31) Preopercle slender and not extending below the quadrate.

Relationships of Group VII

In general the genus Oryzias shows relationships with the world-wide aplocheilids in possessing the following characters:

(a) a very narrow preorbital with a vertical, median, narrow groove running throughout its entire length,

(b) three ossified basibranchials,

(c) short and broad premaxillary processes, and

(d) prominent prezygapophyses which join to enclose canals.

In particular the genus Oryzias shows relationships with the Old World aplocheilids in possessing the following characters:

(e) absence of subcleithral bone, and

(f) absence of a supracleithrum,

In possessing nonprotrusible premaxillaries, enlarged upper and lower pharyngeals with numerous rows of teeth, and external lateral processes in each half of the pelvic girdle, Oryzias shows peculiarities of its own.

In possessing high set pectorals Oryzias resembles aplocheilichthyians (including Lamprichthys).

In the loss of a vomer this genus agrees with the Peruvian genus Orestias.

The characters (a), (b), (e) and (f), however, are peculiar to the Old World aplocheilids and it is from this stock that Oryzias seems to have been derived. In the course of its evolution the genus Oryzias, therefore, seems to have retained certain ancestral characters, acquired its own peculiarities, and come to resemble superficially rather widely separated forms (both aplocheilichthyians and Orestias) with which it is not directly related.

Myers (1931 and 1938) assigned Oryzias as the sole member of the tribe Oryziatini which he (1938) put in the subfamily Fundulinae. Because of the peculiar organization of the genus Oryzias with its nonprotractile jaws and absence of vomer, opinions have been expressed that it may represent a separate subfamily or even a family. In this connection Myers (1958: 28) remarked that "If preliminary results can be believed, the genus Oryzias, which may represent a different subfamily or even a family, has lost even the prevomer itself." Because my observations further support Myers' conclusion, it is suggested that Oryzias be put in the separate family Oryziatidae. This action would recognize not only its distinctive nonprotractile type of jaw but also the geographic entity of the genus.

GROUP VIII

Composition and Range

This group contains a single genus Orestias Cuvier and Valenciennes, with several species all of which seem to be confined to lakes and rivers of Central Peru, Eastern Bolivia and North Central Chile.

The following account is based on Orestias agassizii Pellegrin.

Osteology
(Figs. 52 and 53)

The occipital region of Orestias agassizii is made up of four occipital bones as in other cyprinodonts. The exoccipitals alone form the sides and the dorsal portion of the foramen magnum. The floor of the latter structure is formed by the basioccipital which bears an occipital condyle for articulation with the centrum of the first vertebra. The exoccipital condyles are present, although they are not as conspicuous as in aplocheilids or fundulids. The first vertebra has well-developed articulating surfaces for these condyles but its neural arches are separate from both the supraoccipital and the exoccipitals. Both the jugular and the hypoglossal foramena are normally disposed on the ventral surface and the lateral wall of the exoccipital respectively. The supraoccipital processes extend backward from the dorsal surface of the supraoccipital.

The details of the otic bones are similar to other cyprinodonts. The opisthotic is absent. The anteromesial process of the prootic is present and there is a prominent cartilaginous area between the epiotic, prootic and the frontal on either side.

In the orbitotemporal region the parietals are absent; the frontals are extensive and, in the posterior orbital region, enclose wide notches for the postorbitals. The postorbital, however, is very small and is located toward the anterior surface of the sphenotic process. The supraorbital processes of the frontals are fairly well developed although not to the extent as found in fundulids or aplocheilids. The parasphenoid is normally disposed but its dorso-lateral processes are small and do not extend laterally to meet the alisphenoids, which are located in their normal position. The lachrymals are wide bones located in front of the orbits. The basisphenoid is absent.

The ethmoid region of Orestias agassizii is differently organized from other cyprinodonts except Oryzias. The nasals are found and are located on the dorsal aspect of the skull. As in aplocheilids, the lateral ethmoids are extensive, especially their anterolateral processes. The vomer is absent. The only other genus which lacks a vomer is Oryzias. In this respect these two genera seem to be unique among cyprinodonts. Evidently the vomer has been lost independently in each of them and its absence does not show any direct relationship, for they differ in other important characters which are presently to be mentioned.

Visceral Skeleton

The metapterygoid is absent. The dorsal process of the maxilla is well developed, while the mesial process is small. The lower extremity of the maxilla is rather broad and round. The premaxillary processes are small and pointed at their extremity. They extend backward over the small mesial processes of the maxillae. The premaxillae bear two rows of conical teeth. The autopalatine is normally disposed and bears both the rostropalatine and the ethmopalatine processes. The quadrate is normally disposed. The mesopterygoid is present as in other cyprinodonts. The hyomandibular is elongate and the symplectic is normally disposed.

There are only two ossified basibranchials. The hypohyal is represented by a single piece on each side. In other details the branchial arches tend to resemble the conditions as in Fundulus and its allies. The lower pharyngeals are provided with gill-rakers toward their anterior surfaces. All the four epibranchials are distinct. The first pharyngobranchial is cartilaginous; the second is separate but close to the single plate formed by the union of the third and the fourth pharyngobranchials. There are about 14 gill-rakers on the anterior side of the first gill-arch. All the gill-rakers are pointed as in cyprinodontids and the fundulids. This is in contrast to the aplocheilids where, except for the pointed gill-rakers on the anterior side of the first arch, all the rest are rosette-shaped at their tips.

The basihyal, the urohyal and the hyoid cornu are normally disposed. The hypohyal on either side is represented by a single piece. As in most of the aplocheilids included in this study, both the upper vertical and the lower horizontal portions of the preopercle are broad. The other opercular pieces are normally disposed. There are five branchiostegals on each side; the first group contains only one branchiostegal ray, while the second group has four. The posttemporal is unforked.

Summary of Significant Osteological Characters of Group VIII

Ethmoid Region

(1) Mesethmoid ossified and composed of double laminae.

(2) Vomer absent.

Orbitotemporal Region

(3) Parietals absent.

(4) Posterior myodome absent.

(5) Dorsolateral processes of the parasphenoid small and not meeting the alisphenoids.

(6) Postorbital small.

Occipital Region

(7) Foramen magnum formed only by the exoccipitals and the basioccipital; supraoccipital takes no part in its formation.

(8) Both the basioccipital and exoccipital condyles well developed.

(9) Neural arches of first vertebra separate from skull; first vertebra with a distinct neural spine.

Visceral Skeleton

(10) Metapterygoid absent.

(11) Teeth conical and biserial in *Orestias agassizii*.

(12) Premaxillary processes elongate; extending over the small mesial processes of the maxilla.

(13) Hypohyal on each side represented by a single piece.

(14) Five branchiostegals in *Orestias agassizii*.

(15) Third and fourth pharyngobranchials fused.

(16) Two basibranchials.

Other Regions

(17) Posttemporal unforked.

(18) Transverse processes of precaudal vertebrae elongated.

(19) Pelvic fins absent.

(20) Prezygapophyses prominent and joined to enclose canals.

(21) Preopercle as in most other aplocheilids included in this study.

(22) Anterolateral processes of the lateral ethmoids elongated.

(23) Median hypural single and fan-shaped.

Relationships of Group VIII

The genus Orestias, consisting of several species, seems to be confined to lakes and stagnant portions of the rivers of the high plateaus of Central Peru, Eastern Bolivia, and North Central Chile, but the limits of the distribution are not known. Its point of greatest abundance, both in numbers of individuals and species is Lake Titicaca. It is also found in Lake Poopo, Lake Junin and in smaller lakes, rivers, brooks and ditches of the upper reaches of the Ramis, Urubamba, and Rimac Rivers. The genus occurs at altitudes from 7,000 to 16,000 feet, but population densities are greatest around 12,000 feet (Eigenmann, 1920; Myers, 1951; Eigenmann and Allen, 1942; Berg, 1940 and Techernavin, 1944, give additional distributional data).

Being found only in the highlands and reaching probably the highest altitude inhabited by fishes, the question of the origin and the relationships of this genus has excited much interest. The other species of fish which are found associated with it belong to only those genera which are mountain scalers and are at home in torrents from near sea level to the heights, and they may have worked their way up the present streams. Orestias, on the other hand, is not found in the torrential portions of the streams, but in backwaters, lagoons, swamps, quiet places of the rivers and lakes.

Therefore, it is unlikely that Orestias has managed to climb the presently existing streams. Furthermore, it has no relatives in the lowlands and it has never been found below 7,000 feet. It seems to be an ancient genus whose origin is bound up with the origin of the Andes. It is possible that ancestors of this genus were pushed up by the rise of the Andes, thus isolated from their relatives, which later became virtually extinct in Peru (Eigenmann, 1920, and Eigenmann and Allen, 1942).

The relationships of Orestias have been discussed to some extent along with a similar question about Empetrichthys. A few points, however, need further comment.

Gilbert (1893), Jordan and Evermann (1896), and Eigenmann (1920) hypothesized that Empetrichthys and Orestias were related genera. Jordan (1923: 158) placed these two genera in a distinct family, the Orestiidae. On the other hand, Myers (1931) commenting on the same problem and utilizing some of the skeletal characters, concluded that the two genera were unrelated and placed Empetrichthys in the subfamily Fundulinae and created a separate subfamily Orestiatinae for the sole reception of Orestias. Hubbs (1932: 2) while discussing the relationship of the two genera commented that "There is probably no immediate relationship between Empetrichthys and Orestias, although both were probably derived from some such basic stock as Profundulus . . ."

The diagnostic characters of Orestias, as listed by Regan (1911) and Myers (1931), relate to the bifid or trifid nature of the epipleurals and the absence of parietals. Because the epipleurals are simple in Orestias agassizii, this character cannot be used to diagnose the genus. However, the absence of the parietals, the vomer, and the pelvics, are characters of considerable significance and taken collectively they diagnose the genus from other cyprinodonts.

Among the oviparous cyprinodonts the genus *Orestias* seems to be peculiarly organized in that some of its osteological characters resemble those of the fundulids and the aplocheilids while in other respects it shows peculiarities of its own.

Orestias differs from fundulids (Group III) in the following:

(1) No parietals.

(2) Letaral ethmoids with well-developed anterolateral processes.

(3) Prominent prezygapophyses which join one another dorsally to enclose canals.

(4) First vertebra with a distinct neural spine.

(5) Small postorbital.

(6) Pharyngeal teeth with a slight shoulder as in *Rivulus*.

(7) The shape of the preopercle is more like most of the aplocheilids included in this study.

In the above mentioned characters, *Orestias* not only differs from the fundulids but also appears to resemble the aplocheilids (Group V). It differs from the aplocheilids in the following respects:

(1) Absence of metapterygoid.

(2) Two basibranchials instead of three.

(3) Wide instead of a narrow preorbital (lachrymal).

(4) Hypohyal on each side represented by one instead of two pieces.

(5) Third and fourth pharyngobranchials fused instead of separate.

(6) Ossified instead of a cartilaginous mesethmoid.

(7) Absence of vomer.

In the absence of a vomer, Orestias shows superficial resemblance to the widely separated Oriental genus Oryzias.

It seems, therefore, that with the uplift of the high Andes, an ancestral stock became isolated and subsequently evolved into the genus Orestias. Apparently, the ancestral stock was close to the aplocheilids, because Orestias still possess some of their characters as mentioned above. In the absence of a fossil record, this hypothesis must remain tentative.

Several authors have considered the group of Orestias as a family or a subfamily (Orestiasini Bleeker, 1860; Orestiformes Bleeker, 1863; Orestiinae Gill, 1893; Regan, 1911; Fowler, 1916; Orestiidae Jordan, 1923; Orestinae Starks, 1926; Orestiatinae Myers, 1931; Orestini Berg, 1947). Tchernavin (1944), while revising the genus Orestias, has assigned to it some 20 species, 2 subspecies and three forms of lesser taxonomic significance. He arranged these species into four groups and commented that "There is a good reason to consider Orestias as a group of more than generic significance, which could be divided into several genera." However, he did not name these divisions. The taxonomic implications of the above divisions will be discussed in the final section of this study.

DISCUSSION AND SUMMARY

The osteological findings which have been presented reveal that the oviparous cyprinodonts, currently recognized under the family Cyprinodontidae, contain at least seven and possibly eight phyletic lines of evolution. Each of the seven lines is represented by a group of forms separable from the other groups by a number of osteological features and also by geographical distinctions. It has not been possible, however, to find any major osteological differences between the remaining group, Valencia (Group IV) of the Mediterranean region (Spain), and the fundulids (Group III) of North America despite their widely separated geographic distribution. It is possible new approaches may prove more informative.

The relationships of the eight groups in reference have been discussed (following the presentation of data for each group) and, consequently, it is now possible to venture a summary of osteological characters peculiar to the oviparous cyprinodonts, discuss the paleontological data available for the group, consider ancestral origins, examine evolutionary trends, and mention such taxonomic implications as have become evident.

Major Osteological Characteristics of Oviparous Cyprinodonts

The oviparous cyprinodonts share a number of osteological features in common and these characteristics, taken as a whole, lend support to the integrity of the group. The following attributes were found in each of the forms studied:

(1) Brain case incompletely ossified; small cartilaginous areas persistent in adults; cartilaginous interspaces present between margins of replacing bones.

(2) Maxillae edentulous and not entering gape; biting part of upper jaw formed by premaxillae exclusively.

(3) Orbitosphenoid, basisphenoid, opisthotic and mesocoracoid absent.

(4) Branchiostegals arranged in two groups on each side.

(5) Frontals large and extensive.

(6) First vertebra without ribs and transverse processes (parapophyses); epipleurals attached directly to neural arches.

(7) In remaining precaudal vertebrae, transverse processes present and coossified with centra; ribs present and articulated with transverse processes; epipleurals attached to upper proximal ends of ribs.

(8) Supraoccipital processes present.

Osteological Features Peculiar to Different Groups

In contrast to the shared characteristics, the groups differ from each other in many respects. Some of the more conspicuous variations are listed here in the form of a summary.

Mesethmoid

Two major types of mesethmoids occur in the cyprinodonts under discussion:

(1) Cartilaginous (as found in aplocheilids, aplocheilichthyians, and aphanids), and

(2) Ossified and composed of double laminae (as found in cyprinodontids, fundulids, *Valencia*, *Orestias*, and *Oryzias*).

Anterolateral processes of the lateral ethmoids

These processes are considerably elongated in aplocheilids and in *Orestias* but they are small in all the other groups.

Vomer

The vomer is entirely absent in *Orestias* and *Oryzias*; in all the other groups it is present and devoid of teeth except in the aplocheilids which have a vomer provided with a small patch of conical teeth towards its anterior extremity.

Parietals

These bones are invariably present in fundulids and *Valencia*; invariably absent in cyprinodontids, aphanids, aplocheilichthyians, *Orestias* and *Oryzias*; they are variable, however, in aplocheilids.

Posterior myodome

This structure is variable both between the groups as well as within the groups of cyprinodonts under consideration. In cyprinodontids, aphanids, aplocheilichthyians and *Orestias*, it is invariably absent; in fundulids and aplocheilids, it is present in certain genera but absent in others, and in *Valencia* and *Oryzias*, it is present. Moreover, the structure of the posterior myodome is variable as has been pointed out in connection with the descriptive osteology of Groups III, IV, V and VII.

Parasphenoid

The parasphenoid is well developed in all the groups, but its anterior processes are small and located toward the inner aspect of the parasphenoid in all the genera which lack a posterior myodome (Figs. 8B, 49A, 52B and 54B). In the genera which possess a posterior myodome, the anterior processes of the parasphenoids are long and laterally situated (Figs. 32, 33A and 46).

Alisphenoids

The alisphenoids are small bones and are situated toward the posterolateral corners of the orbits in all the cyprinodonts under consideration (Figs. 8B, 49A, 52B and 54B). These bones are, however, slightly enlarged in all the genera which possess a posterior myodome (Figs. 32, 33A and 46).

Supraorbital processes of the frontals

These processes are small, slightly convex dorsally and do not cover the eyes completely in either the cyprinodontids or in the three fundulid genera (Lucania, Chriopeops and Leptolucania). In all the other genera, these processes are extensive, flattened dorsally and completely cover the eyes.

Notch between the supraorbital process and the sphenotic

In aplocheilids, aplocheilichthyians, and Orestias this notch is very extensive while in all the other genera it is small except in Oryzias which lacks a notch because the sphenotic is in close contact with the supraorbital process of the frontal.

Postorbital

The postorbital is very small in all aplocheilids except Aplocheilus and in Orestias; in all the other groups it is well developed.

Lachrymal (Preorbital)

This bone is wide in all the groups except in the aplocheilids and Oryzias (Group VII) both of which have a characteristically twisted lachrymal medially grooved along its outer border.

Epiotic processes

These processes are present in Oryzias, all fundulids except Adinia and Leptolucania, while they are also absent in all other cyprinodonts.

Supraoccipital

Except in cyprinodontids, in which the supraoccipital extends posteriorly and forms a conspicuous dome-shaped structure over the foramen magnum, this bone stops short of reaching the foramen in all the other groups of cyprinodonts. In other words, in cyprinodontids the foramen magnum is formed by the basioccipital, exoccipitals and the supraoccipital while in all the other groups the foramen magnum is formed entirely by the basioccipital and the exoccipitals.

Exoccipital condyles

The exoccipital condyles are absent in the cyprinodontids while in all the other groups these condyles are well developed.

Premaxillary processes

In cyprinodontids and aphanids the premaxillary processes are typically small and pointed at their tips and they do not extend backward over the mesial processes of the maxillae. In aplocheilids, aplocheilichthyians, and *Oryzias* these processes, although small, are very broad and extend posteriorly over the mesial processes of the maxillae. In fundulids the premaxillary processes are of three types and extend over the mesial processes of the maxillae: small and fairly broad in *Profundulus*, small and narrow in *Empetrichthys* and *Crenichthys*, and long and narrow in *Fundulus*, *Adinia*, *Lucania*, *Chriopeops* and *Leptolucania*. In *Valencia* the premaxillary processes are long and narrow and extend over the mesial processes of the maxillae.

Maxilla and autopalatine processes

In *Oryzias* the upper portion of the maxilla is expanded and supports a similar expansion of the premaxilla from below, thereby making the premaxilla nonprotractile. Moreover, in this genus the two well-developed processes of the autopalatine form a notch into which the maxilla is lodged, thus adding to the nonprotrusibility of the jaws. In all the other groups, the premaxilla, the maxilla and the autopalatine are normally disposed and the jaws are protractile.

Articulation of the skull and vertebral column

In cyprinodontids the skull articulates with the vertebral column through the basioccipital condyle. Moreover, the neural arches of the first vertebra in the cyprinodontids are applied closely to the occipital region to form a strong articulation. In all the other genera the articulation of the skull with the vertebral column is through the basioccipital and the exoccipital condyles. The neural arches of the first vertebra in all these groups remain separate from the occipital region.

First vertebra

As mentioned above the neural arches of the first vertebra are in intimate union with the occipital region in cyprinodontids and therefore the vertebra lacks a neural spine, whereas they are separate from the occipital region in all the other groups. In fundulids (except *Profundulus*, *Empetrichthys* and *Crenichthys*) the neural arches of the first vertebra are not only separate from the occipital region, but they are also separate from one another and do not meet above the neural canal and, therefore, they, too, lack the neural spine. In *Produndulus*, *Empetrichthys*, *Crenichthys* and *Valencia*, although the neural arches of the first vertebra are separate from one another distally, a transverse bony septum connects them just below their tips. In all the other groups the first vertebra has a distinct neural spine.

In all the groups, except cyprinodontids, the first vertebra possesses two corresponding facets, toward its anterior end for articulation with the exoccipital condyles. Such facets are, however, absent in the cyprinodontids.

Posttemporals

The posttemporal is distinctly and invariably forked in cyprinodontids, aphanids, Profundulus, Empetrichthys, Crenichthys and Fundulus kansae; it is variable (forked to unforked) in aplocheilids; it is distinctly unforked in the other fundulids, Orestias, Valencia, aplocheilichthyians and Oryzias.

Branchiostegals

The number of branchiostegal rays in the several genera varies from three to six.

Hypohyal

In aplocheilids the hypohyal on each side is represented by two bony pieces whereas in all the other groups it is composed of a single piece.

Interhyal

Except in Oryzias, which lacks an interhyal, this bone is present in all the other groups.

First pharyngobranchial

The first pharyngobranchial is cartilaginous and devoid of teeth in all the groups except Floridichthys carpio in which it is ossified and possesses two rows of conical teeth.

Third and fourth pharyngobranchials

These are distinctly separate in aplocheilids but in all the other groups they are fused to form a single plate.

Basibranchials

There are three ossified basibranchials in aplocheilids and *Oryzias*; in all the other groups there are only two ossified basibranchials.

Transverse processes of the precaudal vertebrae

These are short and cup-shaped in cyprinodontids; in all the other groups they are elongated.

Median hypural

This structure is trifid in *Aplocheilus panchax*; bifid in the other aplocheilids and *Oryzias*; in *Profundulus*, *Empetrichthys*, *Crenichthys* and *Valencia* it shows indications of division by a median suture; and in the other fundulids, cyprinodontids, aphanids, and *Orestias* it is a fan-shaped piece without external indications of division.

Prezygapophyses

The prezygapophyses are prominent and join dorsally to enclose canals in aplocheilids, *Orestias* and aplocheilichthyians; they are prominent in fundulids, *Valencia*, and *Oryzias*, although not joining dorsally to enclose canals; in cyprinodontids and aphanids the prezygapophyses are small.

Haemal canals

The haemal canals of the first few caudal vertebrae are very wide in aplocheilichthians; less wide in aplocheilids, fundulids, Oryzias, Orestias, and Valencia; and narrow in cyprinodontids and aphanids.

Supracleithrum

Except in Leptolucania, in which the supracleithrum is absent, this bone is present in all genera under consideration.

Pectoral rays

The pectoral rays are set high on the body in aplocheilichthyians (including Lamprichthys tanganicanus), and in Oryzias; in all the other groups they are set low.

Space between coracoid and cleithrum

This space is very wide in aplocheilichthyians (including Lamprichthys tanganicanus), Aplocheilus, and Oryzias; in all the other genera it is narrow.

Cyprinodont Paleontology

Mayr (1953: 42) in a general discussion of Phylogeny and Classification remarked " . . . paleontology and comparative morphology are on the whole the most productive sources of phylogenetic information." It is pertinent, therefore, to review here available paleontological information concerning cyprinodonts before entering into the discussion of a generalized cyprinodont stock, trends of evolution in oviparous cyprinodonts, and taxonomic problems concerning these fishes.

The following list of fossil cyprinodonts has been compiled from a number of sources but principally from Cope (1891), Regan (1911), Eastman (1917), Jordan (1924, 1925), White (1927), Myers (1931), Hibbard and Dunkle (1942), Robertson (1943), Miller (1945), and Berg (1947).

Pachylebias Woodward. Upper Miocene of the Mediterranean region.

Carrionellus White. Lower Tertiary of Ecuador.

Prolebias Sauvage. Oligocene and Miocene of Europe.

Brachylebias Priem. (?) Miocene of Persia.

Poecilops Sauvage. Lower Miocene of France.

Gephyrura Cope. (?) Oligocene of South Dakota.

Proballostomus Cope. (?) Oligocene of South Dakota, possibly as late as Pleistocene, according to Schaeffer as quoted by Rossen and Gordon (1953: 38).

Fundulus (including Parafundulus Eastman) Lacepede. Pliocene and Pleistocene of Lahontan basin (Nevada and California), Pliocene of Death Valley National Monument, California, Mohave Desert, California, and Pliocene of Kansas.

The following species are known:

Fundulus nevadensis (Eastman). Lahontan basin, near Hazen, Nevada.

F. erdisi (Jordan). Lahontan beds of northern Los Angeles County, California.

F. curryi and *F. eulepis* Miller. Death Valley National Monument, Inyo County, California.

F. davdae Miller. Mohave Desert, California. Pliocene or early Pleistocene.

F. sternbergi Robertson. Pliocene of Kansas.

F. detillae Hibbard and Dunkle. Pliocene of Kansas.

Cyprinodon breviradius Miller. Death Valley National Monument, Inyo County, California. Found in the same beds as *F. curryi* and *F. eulepis* (Miller, 1945).

As will be apparent from the following review of the literature, ideas concerning the relationships of fossil cyprinodonts have suffered from a certain amount of confusion. This is not surprising when it is considered that the basis for such relationships, comparative osteological information of living forms, has been altogether absent.

Regan (1911: 323) included *Pachylebias* of the Miocene in the subfamily Cyprinodontinae along with such living genera as *Cyprinodon*, *Lebias* (now *Aphanius*) and *Tellia* (now *Aphanius*). White (1927: 522) described Carrionellus from the (?) Lower Miocene of Ecuador and remarked: "The tricuspid teeth and the absence of secondary sexual characters refer Carrionellus to the Cyprinodontinae of Regans' classification (1911: 325). The multiple row of teeth provides a valid generic distinction from living genera, which is further emphasized by the position and uniformity of dorsal and anal fins." Myers (1931: 12) included both Pachylebias and Carrionellus in the subfamily Cyprinodontinae. Miller (1956: 7-8), on the other hand, thought that Carionellus might not be the member of the subfamily Cyprinodontinae and wrote: "The Tertiary fossil cyprinodontid Carionellus (White, 1927), of Equador, has been included in the Cyprinodontinae because of its tricuspid teeth (in at least two rows rather than a single row), but a study of the published figure indicates that this fish differs importantly from the American genera assigned to this family."

About Prolebias Regan (1911: 325) commented: "The Oligocene and Miocene Prolebias, Sauv., seems to be related to Fundulus; it has 32 to 34 vertebrae (A. S. Woodward, Cat. Foss. Fish. IV p. 290, 1901)." White (1927: 522) agreed that Prolebias "seems to be a true Funduline, . . ." Myers (1931: 10) commented that "Whether or not Prolebias of the Oligocene and Miocene of Europe is nearer to Valencia I can not at present determine, having no material of the fossil genus."

Uncertainty also prevails concerning the systematic position of the other genera. Fundulus cannot be clearly distinguished from living genera and the same applies to the fossil Cyprinodon described by Miller (1945); Gephyrura has a forwardly placed dorsal fin, a small pectoral of nine rays, and seemingly no hypural, although all the living cyprinodonts possess hypurals.

Although not so indicated by Cope (1891), Rosen (1953: 39, Fig. 44), to whom the same skeleton was available, remarked: "Of the structural details of the Proballostomus anal fin skeleton, probably the most important for consideration of intermediate forms in the evolution of specialized reproductive organs are the supporting hemal [sic] spines which have enlarged and rotated forward. These structures may be compared with the comparable elements in the gonopodial suspensorium of the poeciliid, Xiphophorous maculatus (text-fig. 45)." He further states, "In other respects, the anal fin skeleton of Proballostomus compares favorably with those of living cyprinodonts such as Fundulus, but it even appears to be slightly more specialized in the cephalo-caudal extension of its actinostal plates."

Brachylebias from the (?) Miocene of Persia, is said to be near Prolebias and has but twenty-three to twenty-four vertebrae (F. Priem, 1908).

Except that the dorsal fin is opposed to the ventrals, no other useful information is available for the Lower Miocene genus Poecilops which has been reported from France (H. C. Sauvage, 1874).

It is apparent, therefore, that not much palaeontological information can be obtained from the fossil cyprinodonts except in connection with the position of their fins and such meristic characters as the number of fin rays and vertebrae but at times, even this information is lacking. Such meristic characters, as the study of the living forms shows, overlap to a considerable degree and, therefore, can be of only limited value in deciphering the true relationships of the fossil forms. It is also evident that all fossil cyprinodonts need a reexamination in the light of the present study. Too much emphasis seems to have been attached to the general form of the body and to highly variable meristic characters, and too little attention has been paid to more dependable osteological attributes of such items as the metapterygoid, the vomer and its teeth, the basibranchials, the branchiostegals, the premaxillary processes, the parietals, the supraorbital processes, the exoccipital condyles, the first vertebra, the transverse processes, the prezygapophyses, and the hypurals. All of these are important in deciphering the true relationships of fossil forms and it is hoped that the present study will provide such a basis for reevaluating the relationships of the fossil forms. If this is done then our knowledge of the evolution of the cyprinodonts and their relationships with other groups of fishes will be enhanced.

In the absence of pertinent paleontological information, it would indeed have been a hopeless task to construct the phylogeny of the oviparous cyprinodonts had the study not revealed rather distinct evolutionary lines within the several living groups of these fishes. Moreover, certain genera seem to have retained some of the ancestral characters in spite of many modifications in other respects. Certain genera (Aplocheilus, Epiplatys and Rivulus) appear to be bradytelic lines representing fairly well the ancestral stocks.

Ancestral Cyprinodont Stock

In the lack of palaentological data and the absence of osteological information about the living forms, it seems that almost all the views which have been expressed about a generalized ancestral cyprinodont stock have been more or less premature. Hubbs (1924: 12) on the basis of certain external characters of Profundulus came to the conclusion that this genus was the most generalized cyprinodont. In this connection he remarked: "As the more generalized members of the Fundulus, Cynolebias and some other American genera of the Cyprinodontidae, as well as the less specialized Goodeidae resemble the species of Profundulus in habitus, it seems not improbable that Profundulus, of all American genera, diverges least from a general ancestral cyprinodont type. The geographical distribution of the groups in question harmonizes with such a view." The chief characters which he cited for his conclusions are:

(1) the absence of a genital pouch in the adult females of Profundulus, and

(2) the dorsal and anal fins are relatively long and low, the anal composed of more rays (15-17).

The first of these characters could be considered to be generalized and present in the primitive and ancestral cyprinodont but the second character seems to be untenable. The anal fin is quite long in many other genera of cyprinodonts: Procatopus has 15 to 17, Hypsopanchax has 14 to 21, Aplocheilus has 17, Rivulus and Oryzias have 16 to 18, and Lamprichthys has 30 anal rays. Profundulus, as has been shown in this study, seems to have been derived from some aplocheilid stock, the present-day members of which seem to be the most generalized forms and, therefore, a generalized cyprinodont type should be searched for within the aplocheilids (Group V). Although Profundulus does not represent the most generalized type, it nevertheless seems to be the most primitive living genus among the North American cyprinodonts.

Myers (1931: 249), on the other hand, implied that Valencia was the most generalized of all genera when he remarked: " . . . this genus may represent the ancestral stock from which Rivulini [Aplocheilini] have sprung." He, however, did not list characters for the basis of such a conclusion except that the preorbital is reduced in this genus as in aplocheilids. It is now clear that it has been just the opposite case, i.e., not that Valencia gave rise to aplocheilids but that a stock similar to the aplocheilids gave rise to Valencia. Myers (1958: 28), however, seemed to have modified his views recently when he remarked that, " . . . instead the Oriental genus Aplocheilus presents by far the largest number of basic characters that have become specialized or even lost in other members of the family." In view of my study of a wide range of representative material of oviparous cyprinodonts, I tend to agree with this recent statement of Myers that Aplocheilus seems to be the most generalized cyprinodont. In order to be more conclusive, however, the genera which have not been included here need to be investigated, and also a better knowledge of the cyprinodonts of both Africa and South America is necessary. I cite below the basis of my conclusions that Aplocheilus and other similar aplocheilids (Group V) are the most generalized among the order Cyprinodontiformes.

The group of cyprinodonts composed of such genera as Aplocheilus in Asia; Epiplatys, Aphyosemion and Nothobranchius and others in Africa; Rivulus, Cynolebias and others in Central and South America form a homogeneous unit. All of these genera possess osteological characters which seem to have been either dropped or modified in different lines of evolution in different parts of the world. They all possess a comparatively enlarged vomer and a patch of vomerine teeth, a metapterygoid, a cartilaginous mesethmoid, distinct exoccipital and basioccipital condyles, short and broad premaxillary processes, jaws with conical teeth arranged in a band, hypohyal on each side represented by two bony pieces, usually six branchiostegal rays, separate third and fourth pharyngobranchials, three ossified basibranchials, posteriorly directed bony processes of the pelvic bones small, prominent prezygapophyses which meet dorsally to enclose canals, median hypural bifid or trifid, and a well-defined neural spine on the first vertebra.

Adding to the above list certain other generalized characters such as the relatively low position of the pectoral fins, adaptability to different ranges of salinity, and the perennial nature of most of the species, provides a sort of 'character pool' for this generalized basic group. This group would then seem to have given rise to other groups through modification of certain characteristics and through the elimination of others.

It is pertinent here to draw upon the facts of geographical distribution of aplocheilids and other groups, for if such facts harmonize with the anatomical findings, they would supplement and strengthen each other.

The distribution of the aplocheilids is a southerly one, principally African and South American. In this respect the group resembles the southern peripheral distribution of the more primitive members of many groups of terrestrial and fresh water vertebrates. *Aplocheilus*, according to Myers (1958: 28) and also according to my study, is the most generalized genus of the group, and has a distribution (in Southern Asia) peripheral to its closest relatives in Africa and apparently it has not inhabited India and Malaya for long. Since, moreover, other genera of aplocheilids, both in Africa and South America, agree rather closely in their osteological features, it is entirely possible that the cyprinodonts originated somewhere near Africa, most probably around the Tethys Sea which exists at present in remnant form as the Mediterranean Sea. From such a center they could have spread to different parts of the world and there given rise to the different groups. How this dispersal took place, across the shallow coastal areas to Asia and then across the Bering Sea to North and South America, or from Africa to South America through a narrow filter bridge or through a direct land connection between Africa and South America, is a question which must await additional information. The hypothesis that the cyprinodonts originated somewhere around the Tethys Sea is supported by the large number of fossil cyprinodonts found in the Mediterranean region (Steinitz, 1951) and also by the distribution of the aplocheilids as mentioned previously. Kosswig (1943) advanced a similar hypothesis in his contention that the present-day Mediterranean cyprinodonts represent a Tethys faunal relict, in order to explain the distribution of these cyprinodonts. Steinitz (1951), while discussing the distribution and evolution of the cyprinodont fishes of the Mediterranean region and the Near East, brought forward further evidence in support of Kosswigs' hypothesis. It is obvious, however, that much additional information will be necessary on both the living and the fossil cyprinodonts before concrete conclusions can be reached relative to their distribution and dispersal in the past.

Evolutionary Trends

The following patterns are discernible from the present study as regards the trends of evolution in the oviparous cyprinodonts:

Loss of mobility of maxillae

In all generalized teleosts the maxillae are moveable and lie freely exposed on both sides of the head. This is also the case in the Oriental genus Aplocheilus, but in the African genus Epiplatys the maxilla has become partly embedded in the flesh of the preorbital region. This bone is, however, completely embedded and practically immovable in all the other cyprinodonts examined in this study. Further, in Oryzias the structure and relationships of the maxillae and the premaxillae are such that the entire mouth is nonprotrusible.

Reduction and modification of teeth

In aplocheilids the premaxilla and the dentary are provided with a band of conical teeth, but in several genera the teeth have been reduced to two rows as in *Chriopeops*, or to one row as in *Lucania*. In other lines the conical teeth have become bicuspid as in *Crenichthys* or tricuspid as in cyprinodontids and aphanids. The evolution of the tricuspid teeth has, however, occurred independently on two occasions, once in the New World cyprinodontids (Group I) and again in the Old World aphanids (Group II).

Loss of vomerine teeth and vomer

The vomer is a large bone in aplocheilids and bears a patch of teeth towards its anterior end. These teeth have, however, been lost in all other cyprinodonts. In the Oriental genus *Oryzias* and in the Peruvian genus *Orestias* even the vomer has been lost. Again the loss of the vomer seems to have occurred independently in these geographically separated and unrelated genera.

From low set pectorals to high set pectorals

In all the more primitive teleosts the pectoral fins are inserted low on the sides of the body. They also are set relatively low in aplocheilids. From this position, trends toward high-set pectorals are present in the Oriental genus *Oryzias* and the African aplocheilichthyians (including *Lamprichthys*).

Changes in body form

In general the cyprinodonts are more or less elongated and cylindrical with a short, round, and moderately depressed head, and the dorsal fin is located far back with its insertion behind that of the anal as in Aplocheilus and in Rivulus. In different specialized lines, however, the head and the body show deepening and compression as in Cyprinodon, Adinia, Procatopus and Lamprichthys, and the dorsal fin is located in the middle of the body or may even originate in advance of the anal fin as in Cyprinodon, Floridichthys and Jordanella.

Changes in the occipital region and the first vertebra

In general (Groups II, V, VI, VII and VIII) the basioccipital forms the floor of the foramen magnum while the exoccipitals form the side walls and the roof of this structure and both the basioccipital and the exoccipitals bear condyles for articulation with the first vertebra. The supraoccipital stops short of reaching the foramen magnum and takes no part in its formation. The first vertebra has a distinct neural spine and its neural arches are separate from the occipital region. In Fundulus and Valencia (Groups III and IV), although the occipital region is constructed on the same pattern as described above, the first vertebra lacks a neural spine because its neural arches have become free and do not meet above the neural canal. In Cyprinodon and its allies (Group I) the supraoccipital extends posteriorly to form a conspicuous dome-shaped structure over the foramen magnum; also the exoccipital condyles are absent and the neural arches of a spineless first vertebra are applied to the occipital region, where these neural arches share in the articulation of the skull and the vertebral column.

Changes in scalation

The cyprinodonts usually have cycloid scales on both the head and the body. In *Kosswigichthys asquamatus*, however, the scales have been lost entirely and in *Lamprichthys tanganicanus* the scales have become ctenoid.

Reduction and loss of pseudobranchiae

The pseudobranchiae are present but poorly developed in the aplocheilids (Group V); in all the other groups they have been lost completely.

Changes in breeding behavior and life cycle

Most cyprinodonts are perennial fishes which live for three or four years. This is also true for the aplocheilids in general but within this group several genera in South America and Africa have become annuals adapted to life in isolated pools and mudholes which dry up once a year. The population then exists solely as fertilized eggs buried in damp mud under a hard dry top crust.

From the foregoing account and from the consideration of the relationships of the different groups of the oviparous cyprinodonts, it is evident that the loss of various bony elements and the modification of others is conspicuous in the evolution of the several lines of descent. Because the aplocheilids possess the bony elements in full array and are also distributionally the most cosmopolitan, it is reasonable to conclude that they form the basic stock from which other groups of cyprinodonts arose in different parts of the world.

The superficial resemblances which these groups show to one another are due to parallel evolution for, otherwise, these groups form separate and well-defined, phyletic entities.

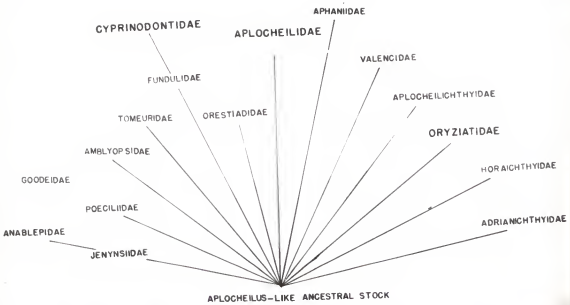
The phylogeny of the oviparous cyprinodonts, as indicated by the present study, is shown in the accompanying dendrogram. On the basis of the results of others, the remaining families of the order have also been included in it. The entire arrangement, however, is tentative and must remain so until all the groups, both viviparous and oviparous, have been compared and analyzed on the basis of dependable assemblage of common characteristics.

Taxonomic Implications

The findings of the present study suggest a number of changes pertinent to the classification of the oviparous cyprinodonts, until now included in the family Cyprinodontidae. These can best be appreciated in the taxonomic background of the group, which is given below:

Regan (1911) published a classification of the order Microcyprini (=Cyprinodontiformes) and separated its various taxa into two suborders: 1. Amblyopsoidea (=Amblyopsoidei Berg) and 2. Poecilioidea (=Cyprinodontoidei Berg), the former containing the family Amblyopsidae and the latter including the family Poeciliidae. He further subdivided the family Poeciliidae into seven subfamilies: 1. Cyprinodontinae, 2. Fundulinae, 3. Orestinae, 4. Characodontinae, 5. Jenynsiinae, 6. Anablepinae, and 7. Poeciliinae.

Jordan (1923) suggested that more families of Microcyprini (Cyprinodontiformes) should be recognized and, therefore, he raised



Dendrogram showing the relationships of cyprinodont fishes (tentative arrangement).

several of Regan's (1911) subfamilies to family status and erected a few new ones for a total of ten: 1. Cyprinodontidae, 2. Orestiidae, 3. Characodontidae, 4. Goodeidae, 5. Poecilidae [sic], 6. Fitzroyidae, 7. Anablepidae, 8. Phallostethidae, 9. Amblyopsidae, and 10. Adrianichthyidae.

Hubbs (1924: 4) agreed with Jordan's (1923) classification of the order Cyprinodontes on the whole, but proposed certain modifications in its details. He pointed out that "The Characodontidae and Goodeidae should not be separated, for to do so would destroy the extreme naturalness of the combined group. The name Characodontinae is synonymous with Goodeinae, which is the older; the family should therefore be named Goodeidae." Further, he proposed that the Fitzroyidae and Anablepidae probably should be reduced to subfamily rank for, according to him, the latter group probably was derived from the former, and that the name Anablepidae holds for the combined group, being the older. Moreover, he pointed out that the name Fitzroyinae must be altered to Jenynsiinae, according to the international rules. The families which Hubbs (1924) recognized in the order Cyprinodontes are: 1. Cyprinodontidae, 2. Adrianichthyidae, 3. Goodeidae, 4. Anablepidae, 5. Poeciliidae, 6. Phallostethidae, and 7. Amblyopsidae. However, neither Jordan (1923) nor Hubbs (1924) delimited these families into two suborders (Amblyopsoidea and Poecilioidea) as Regan (1911) had done before them.

Myers (1928) demonstrated that the Phallostethidae were not members of the order Cyprinodontiformes, and later, while proposing a general classification of the oviparous cyprinodonts, he (1931) followed Regan (1911) in recognizing two suborders (Amblyopsoidea and Poecilioidea), but delimited these fishes into six families: 1. Cyprinodontidae, 2. Adrianichthyidae, 3. Goodeidae, 4. Poeciliidae, 5. Jenynsidae, and Anablepidae. Further, he subdivided Cyprinodontidae into four subfamilies: 1. Fundulinae, 2. Lamprichthyinae, 3. Orestiastinae, and 4. Cyprinodontinae. Moreover, Myers (1931) subdivided Fundulinae into four tribes: 1. Fundulini, 2. Rivulini, 3. Aplocheilichthyini and 4. Aplocheilini. Later he (1938: 137) proposed certain nomenclatorial changes and renamed the tribe Rivulini as Aplocheilini and Aplocheilini as Oryziatini. About Adrianichthyidae he (1931: 7) commented: "They differ considerably from the other families, and may perhaps be viviparous." However, in contrast to Hubbs (1924), Myers (1931) recognized Jenynsidae and Anablepidae as separate families.

Similarly Berg (1947), following Regan (1911), recognized both the suborders Amblyopsoidea and Poeciliodea but erected two superfamilies, Cyprinodontoidae and Poecilioidae, to accommodate the oviparous families (Cyprinodontidae and Adrianichthyidae) in the former and the viviparous families (Goodeidae, Jenynsidae, Anablepidae and Poeciliidae) in the latter. Berg then followed Myers (1931) in subdividing the family Cyprinodontidae into the four subfamilies mentioned above.

Kulkarni (1940) erected a new family Horaichthyidae to receive <u>Horaichthys</u> <u>setnai</u>, a cyprinodont fish which he had discovered near Bombay (India). These fishes are remarkable in that, although oviparous, the males possess a complicated gonopodium formed by the modification of a few anterior anal rays.

An analogous situation exists in the tropical American species Tomeurus gracilis which was long confused with the viviparous Poeciliidae but it was eventually discovered to be oviparous. The males possess a complicated gonopodium which is utilized, as in the case of Horaichthys setnai, to transfer spermatophores from males to females. Concerning the structure of the gonopodium of Tomeurus gracilis Rosen and Gordon (1953: 41) remarked: "Our studies of the gonopodial details of Tomeurus indicate that its functional relations also may be quite different from those of poeciliids." Similarly Myers (1947) was much impressed by the structural peculiarities of Tomeurus and suggested that it may have originated independent of the main line of poeciliid evolution. Both Myers (op. cit.) and Hubbs (quoted by Kulkarni, 1940: 384; Rossen, 1953: 41) proposed that the species under consideration be placed in a separate family Tomeuridae. In the meantime Nikolskii (1954) for the first time but following Myers (1947) and Hubbs (as quoted by Kulkarni, 1940: 384; Rosen and Gordon, 1953: 41), delimited Tomeurus gracilis in a separate family (which he misspelled Tomeiuridae). Further Nikolskii (1954) was so impressed by the uniqueness of this species that he included the family Tomeuridae in a separate superfamily Tomeiuroidae (again he misspelled the basic term).

The above consideration of the two unrelated but oviparous families Horaichthyidae and Tomeruidae in which the males are provided with gonopodia structurally and functionally different from the viviparous families (Goodeidae, Jenynsidae, Anablepidae or Poeciliidae), focusses our attention on the question of the relationships of these two families with the other families of cyprinodonts, both oviparous and viviparous. Evidently, until the relationships of all cyprinodont families are correctly established on the basis of characteristics shared by all, grouping them into larger categories (e.g. superfamilies) as has been done by Berg (1947) and Nikolskii (1954) is premature. From Berg's (op. cit.) classification of the suborder Poecilioidea (=Cyprinodontoidei Berg) into two superfamilies, one containing all the oviparous families and the other containing all the viviparous families, it appears as if all the viviparous families are phylogenetically related but this is not the case. In this connection the remarks of Hubbs (1924: 6) are pertinent: "The gonopodium is the chief distinctive feature of the Poeciliidae (as here delimited). In the other groups of viviparous cyprinodonts the anal fin, to be sure, is also modified as an intromittent organ, but in so different a fashion as to indicate an entirely independent origin as compared with the gonopodium. It is highly probably that the Goodeidae, Poeciliidae, and Anablepidae . . . originated independently from the oviparous Cyprinodontidae. It, is therefore, probable that viviparity has been independently acquired four times among the cyprinodont fishes. If this view is correct, we have in the present case a most striking example of the independent attainment, within one group of animals, of one end through diverse adaptations. The oviparous cyprinodontidae, it would further follow, have had and probably still possess the potentiality of developing viviparity. In fact, many of the species of this family show an approach toward the viviparous condition in the development of clasping structures and habits (see Newman 1907)."

In view of the above considerations I am recommending that the delimitation of the families of cyprinodonts in two superfamilies, chiefly on the basis of their mode of reproduction as has been done by Berg (1947) and Nikolskii (1954) be abandoned until their natural relationships have been established.

Regarding the recognition of two suborders, Amblyopsoidea and Poecilioidea, in the order Cyprinodontiformes as first proposed by Regan (1911) and later adopted by Myers (1931) and Berg (1947), it seems that, although there is no doubt that the amblyopsids and the poecilioids represent two divergent evolutionary lines and, therefore, the above mentioned two groupings are sound, there is a need for revision of the present distinguishing characters of the suborder Poecilioidea. The skeletal characters thus far considered to be diagnostic of the suborder Poecilioidea are not universally applicable to all representatives of the group. Starks (1904) mentioned the presence of a circular scale-like ethmoid (mesethmoid) and the absence of a metapterygoid as the two diagnostic features of the superfamily Poecilioidea. Regan (1911), in his classification of the order Microcyprini considered the absence of the metapterygoid and the ankylosed nature of the palatine and the pterygoid as the two diagnostic features of the suborder Poicilioidea in contrast to the presence of the metapterygoid and the separate condition of the palatine and the pterygoid in the suborder Amblyopsoidea. Both Myers (1931) and Berg (1947) concurred with this view.

The present investigation reveals, however, that the absence of the metapterygoid and the ankylosed nature of the palatine and the pterygoid cannot be regarded as distinguishing characters of the suborder Poecilioidea, because the metapterygoid invariably is present in the aplocheilids (Group V) and the palatine and the pterygoid are distinct in all the cyprinodonts examined in this study. The metapterygoid is absent, however, in all the other groups as delimited here.

Further, the structure of the mesethmoid in the Groups II, V, and VI is unique. In these groups the mesethmoid is an independent piece of cartilage rather than the thin scale-like bone. The thin scale-like ossified mesethmoid, composed of double laminae, is present, however, in Groups I, III, IV, VII and VIII. This indicates that Group V (aplocheilids) is differently organized among the cyprinodonts both in the possession of a distinct metapterygoid and in having a cartilaginous mesethmoid. This conclusion is further supported by the fact that the aplocheilids possess three basibranchials, distinct third and fourth pharyngobranchials, varying parietals (present, indistinct or absent), varying posttemporals (slightly forked, half-way forked or unforked), and bifid or trifid median hypurals.

Regan (1911) characterized the order Microcyprini as having a forked posttemporal but this bone is unforked in many fundulids (Group III), <u>Valencia</u> (Group IV), and <u>Oryzias</u> (Group VIII). The posttemporal is invariably forked, however, in <u>Cyprinodon</u> and related genera (Group I), <u>Aphanius</u> and related genera (Group II), certain fundulids (Group III), certain aplocheilids (Group V) and <u>Orestias</u> (Group VII).

This study has revealed at least seven distinct phyletic lines, within the oviparous cyprinodonts, well separable from one another in numerous osteological characters. Since these seven groups also form well-defined geographical units, I am raising each to a family level. <u>Valencia</u> (Group IV) seems to represent an eighth phyletic line, well-defined geographically but resembling the fundulids osteologically. Because of the lack of differentiating characters, I am tentatively including <u>Valencia</u> with the fundulids.

A synopsis of the seven families of oviparous cyprinodonts together with their diagnostic characters is given below and it seems as if Jordan (1923: 158) had already anticipated this action when he remarked: "Hitherto the viviparous and oviparous cyprinodonts have been placed in a single family, but the differences within the group are extensive and if the species were not all of small size they would certainly be assigned to two or more groups."

Synopsis of the Families of Oviparous Cyprinodonts

I. Exoccipital condyles present; supraoccipital not extending backward to form a dome-shaped structure over the foramen magnum; neural arches of the first vertebra separate from the occipital region and take no part in the articulation of the skull with the vertebral column; no distinct gap between the first and the second vertebrae.

  A. Metapterygoid present; vomer dentigerous; mesethmoid cartilaginous; notch between the supraorbital process of the frontal and the sphenotic wide; lachrymal very narrow, usually with a vertical groove running down its middle; pseudobranchiae present; parietals variable (present, absent or indistinct)

      1. Aplocheilidae, new family.

  B. Metapterygoid absent; vomer edentulous; mesethmoid cartilaginous; notch between the supraorbital process of the frontal and the sphenotic narrow; lachrymal wide; pseudobranchiae absent; parietals absent

    1. Pectorals set high; teeth conical

      2. Aplocheilichthyidae, new family

    2. Pectorals set low; teeth usually tricuspid

      3. Aphaniidae, new family

C. Metapterygoid absent; notch between supraorbital process of the frontal and the sphenotic narrow or absent; lachrymal wide; mesethmoid ossified and composed of double laminae; parietals absent; vomer absent

   1. Pectorals set high; median hypural bifid; notch between the supraorbital process of the frontal and sphenotic absent; jaws nonprotrusible

      4. Oryziatidae, new family.

   2. Pectorals set low; median hypural fan-shaped with only a slight indication of division; notch between the supraorbital process of the frontal and the sphenotic wide; jaws protrusible

      5. Orestiadidae, new family.

D. Metapterygoid absent; vomer edentulous; notch between supraorbital process of the frontal and the sphenotic narrow; lachrymal wide; mesethmoid ossified and composed of double laminae; parietals present; vomer present

      6. Fundulidae, new family.

II. Exoccipital condyles absent; supraoccipital extending backward to form a distinct dome-shaped structure over the foramen magnum; neural arches of the first vertebra applied to the occipital region and take part in the articulation of the skull and the vertebral column; a distinct gap between the first and the second vertebrae

7. Cyprinodontidae, Gunther, 1866.

In the above synopsis only a few diagnostic characters have been mentioned, but additional differences between the various families have already been listed previously.

CONCLUSIONS AND RECOMMENDATIONS

1. Properly evaluated groups of osteological characteristics constitute more dependable evidence of phyletic relationships among oviparous cyprinodont fishes than do single characters.

2. The forked nature of the posttemporal cannot be cited as characteristic of the order Cyprinodontiformes because this bone is unforked in many groups of cyprinodonts.

3. The distinguishing characteristics of the suborder Poecilioidea need revision because the skeletal features thus far considered to be diagnostic of this suborder are not applicable to all members of the group.

4. The absence of the metapterygoid cannot be regarded as a distinguishing character of the suborder Poecilioidea because the metapterygoid is invariably present in all the aplocheilids examined in this investigation.

5. The oviparous cyprinodonts share a number of osteological characteristics in common and, taken as a whole, these characteristics substantiate the validity of the group as a natural assemblage of related forms.

6. Phylogenitically, the viviparous cyprinodonts may be a part of the oviparous cyprinodont assemblage and, therefore, it is recommended that the use of superfamilies Cyprinodontoidae and Poecilioidae be abandoned pending the establishment of the relationships

between the viviparous and oviparous forms on the basis of characteristics other than the single criterion of reproductive method.

7. Osteological characteristics and geographical distribution of the aplocheilids strongly suggest that they are the most generalized of the cyprinodonts.

8. The aplocheilids or a stock similar to them almost certainly represent the ancestral stock from which all other major groups of both the oviparous and the viviparous cyprinodont fishes have originated.

9. Aplocheilus of Asia, Rivulus of South and Central America, and probably Epiplatys of Africa appear to be the most generalized of the aplocheilids.

10. It is suggested that the cyprinodonts probably originated somewhere near the African border of the Tethys Sea which exists at present in remnant form as the Mediterranean Sea.

11. Except for cyprinodontids (family Cyprinodontidae) which probably originated from fundulids (family Fundulidae), all other groups of oviparous cyprinodonts (families Aplocheilichthyidae, Aphaniidae, Oryziatidae, Orestiadidae, and Fundulidae) have evolved from Aplocheilidae or a stock similar to them.

12. As previously recognized, the family Cyprinodontidae is a heterogeneous assemblage containing at least seven and possibly eight distinct lines of evolution. Seven of these lines are separable from one another by a number of osteological characters and also by geographical distinctions.

15. It is recommended that the family Cyprinodontidae, as previously understood, be reorganized into the following seven families:

Aplocheilidae, new family.

Genera: *Aplocheilus*, *Aphyosemion*, *Rivulus*, *Cynolebias*, *Austrofundulus*, and *Nothobranchius* and possibly *Epiplatys*, *Pachypanchax*, *Rachovia*, *Pterolebias*, *Trigonectes*, *Rivulichthys*, *Neofundulus*, and *Hubbsichthys* which were not examined.

Aplocheilichthyidae, new family.

Genera: *Aplocheilichthys*, *Micropanchax*, and *Lamprichthys* and possibly *Hypsopanchax*, *Procatopus*, *Cynopanchax*, and *Plataplocheilus* which were not examined.

Aphaniidae, new family.

Genera: *Aphanius*, *Aphaniops*, *Anatolichthys*, and *Kosswigichthys*.

Oryziatidae, new family.

Genus: *Oryzias*.

Orestiadidae, new family

Genus: *Orestias*.

Fundulidae, new family.

Genera: *Fundulus*, *Lucania*, *Adinia*, *Chriopeops*, *Leptolucania*, *Empetrichthys*, *Crenichthys*, *Profundulus*, and *Valencia*? (see item 16), and possibly *Cubanichthys*, and *Oxyzygonectes* which were not examined.

Cyprinodontidae, Gunther, 1866.

Genera: Cyprinodon, Floridichthys, Jordanella, Garmanella, and Cualac.

14. It is recommended that the family Aplocheilichthyidae be divided into two subfamilies as follows:

Aplocheilichthyinae, new subfamily.

Genera: Aplocheilichthys, Cynopanchax, Plataplocheilus, and Micropanchax.

Procatopinae, new subfamily.

Genera: Procatopus, Lamprichthys, Hypsopanchax, and Platypanchax.

15. The erection of a separate subfamily for the sole reception of Lamprichthys, chiefly on the basis of its ctenoid scales and its numerous vertebrae, is untenable because such a treatment ignores the overwhelming similarities which this genus shares with such aplocheilichthyians as Procatopus, Hypsopanchax, and Platypanchax. Therefore, these four genera are placed into one subfamily, Procatopinae, of the family Aplocheilichthyidae.

16. Lamprichthys tanganicanus appears to be a modified descendent of an aplocheilichthys-like ancestor which perhaps gained access into Lake Tanganyika when it was formed in the Rift Valley during the Pliocene.

17. Valencia is tentatively included in the family Fundulidae but it is suggested that further anatomical studies may show that this genus also represents a distinct phyletic line. Osteologically, Valencia resembles Profundulus more closely than it does other fundulids

and both of these genera have been shown to be generalized primitive types. Therefore, it is suggested that some widespread ancestral stock, structurally resembling the widely distributed aplocheilids of today, entered the fresh waters of Central America and Spain to later produce in those areas Profundulus and Valencia respectively.

18. Within the family Fundulidae two, and possibly three, evolutionary lines are apparent on the basis of osteological characteristics. Therefore, on further study, it may be possible to subdivide the family Fundulidae into three groups as follows:

Group 1 consisting of such genera as Profundulus, Empetrichthys, and Crenichthys.

Group 2 consisting of such genera as Fundulus and Adinia.

Group 3 consisting of such genera as Lucania, Chriopeops, and Leptolucania.

19. Due to the close resemblance of Central American genus Profundulus and the Death Valley genera Empetrichthys and Crenichthys, and the possibility that fossil cyprinodonts known from the Middle Pliocene of Kansas may belong to Profundulus rather than to Fundulus, it is concluded that Profundulus, or a stock similar to it, was distributed from the Mexican Plateau to Death Valley at least in the Middle Pliocene or perhaps earlier. This stock differentiated on the one hand into such closely related genera as Profundulus, Empetrichthys, and Crenichthys, and on the other into Fundulus. From Fundulus were derived two stocks:

(a) Cyprinodon and its allies of the family Cyprinodontidae, and

(b) the Adinia-Lucania group of the family Fundulidae.

20. Lucania parva, Chriopeops goodei (=Lucania goodei of of several recent authors) and Leptolucania ommata are closely related genera and it is suggested that Lucania parva differentiated in Florida to form two strictly fresh water species, Chriopeops goodei and Leptolucania ommata.

21. Although the foregoing phyletic trends are apparent from this study, a more exhaustive study is recommended to determine the precise relationships of various genera of Group III (family Fundulidae). More information is needed concerning the fossil record, a more thorough coverage of representative species, especially of the genera Fundulus and Profundulus, is necessary, and for all forms, more data are required on the comparative osteology, embryology, and anatomy of the soft parts.

22. A number of new osteological characters have been found to distinguish the two genera Empetrichthys and Crenichthys and it is shown that the use of the epipleurals to distinguish these two genera is not applicable.

23. Although showing superficial resemblances, the New World genera with tricuspid teeth (family Cyprinodontidae) and the Old World genera with tricuspid or unicuspid teeth (family Aphaniidae) are not directly related because they differ in many fundamental osteological

characteristics. Their superficial resemblances are to be interpreted as a result of parallel evolution.

24. New World genus *Orestias* (family Orestiadidae) and the Old World genus *Oryzias* (family Oryziatidae) are unique among cyprinodonts in lacking a vomer. Evidently the vomer has been lost independently in each of these genera and, therefore, this character cannot be used to show any direct relationship between them.

25. The dendrogram constructed to show relationships of all the families of cyprinodonts, both oviparous and viviparous, is an arrangement which must remain tentative until all the families have been analyzed on the basis of dependable and comparable assemblages of characteristics.

26. In the course of osteological studies of cyprinodont fishes by previous workers, several errors have accumulated for various reasons. Corrections of these errors are as follows:

(a) It was understood that the cyprinodonts had a circular, scale-like, ossified mesethmoid composed of double laminae as found in *Valencia*, *Orestias*, *Oryzias*, and the fundulids. A second type, entirely cartilaginous, is present, however, in aplocheilids, aplocheilichthyians, and Aphanids.

(b) The suborder Poecilioidea has been characterized by the absence of metapterygoid and the ankylosed nature of the palatine and the pterygoid. The metapterygoid is present, however, in *Aplocheilus*, *Aphyosemion*, *Rivulus*, *Cynolebias*, *Austrofundulus*, and *Nothobranchius*, and the palatine and the pterygoid are distinct in all the cyprinodonts examined in this study.

(c) It was understood that the aplocheilids invariably possessed parietals, but these bones are absent in *Nothobranchius* and indistinct in *Austrofundulus* and *Aphyosemion*. The parietals are, however, present in *Rivulus* and *Aplocheilus*.

27. In this study a number of previously unreported osteological attributes have been discovered for the oviparous cyprinodonts and of these additions several, considered of significance in determining the phylogenetic relationships, are listed below:

(a) The basisphenoid is absent in all the cyprinodonts examined in this study.

(b) The epipleurals are attached directly to the neural arches of the first vertebra because this vertebra lacks both ribs and transverse processes.

(c) The postorbital is very small in all aplocheilids (except *Aplocheilus*) and in *Orestias*; in all other cyprinodonts included in this study it is well developed.

(d) Two arrangements of the supraoccipital bone have been found in this study: In cyprinodontids (family Cyprinodontidae) the supraoccipital extends posteriorly and forms a prominent dome-shaped structure over the foramen magnum, but in all other groups (families: Aplocheilidae, Aplocheilichthyidae, Aphaniidae, Orestiadidae, Oryziatidae, and Fundulidae) the supraoccipital stops short of reaching the foramen magnum and, consequently, takes no part in its formation.

(e) The exoccipital condyles are absent in the family Cyprinodontidae; in all other families of oviparous cyprinodonts these condyles are well developed.

(f) In the family Cyprinodontidae the skull articulates with the vertebral column by the basioccipital condyle and the neural arches of the first vertebra; in all other families of oviparous cyprinodonts the articulation is by the basioccipital and the exoccipital condyles and the neural arches take no part in the articulation.

(g) The number of branchiostegal rays in the several genera examined in this study varies from three to six.

(h) In the family Aplocheilidae the hypohyal on each side is represented by two bony pieces whereas in all the other families of oviparous cyprinodonts it is composed of a single piece.

(i) In <u>Floridichthys</u> <u>carpio</u> the first pharyngobranchial is ossified and possesses two rows of conical teeth; in all other cyprinodonts examined in this study, this element is cartilaginous and edentulous.

(j) In aplocheilids the third and fourth pharyngobranchials are distinctly separate.

(k) In aplocheilids and Oryzias there are three ossified basibranchials.

(l) The transverse processes of the precaudal vertebrae are short and cup-shaped in the family Cyprinodontidae; in all the other families of oviparous cyprinodonts they are elongated.

(m) Median hypural varies from a median fan-shaped element to a bifid or a trifid element.

(n) Three types of prezygapophyses are present in the oviparous cyprinodonts.

(o) Haemal canals are narrow in the families Cyprinodontidae and Aphaniidae; moderately wide in the families Aplocheilidae, Fundulidae, Oryziatidae, Orestiadidae, and in Valencia; and very wide in the family Aplocheilichthyidae.

(p) The supracleithrum is absent in Leptolucania; in all other oviparous cyprinodonts examined during this study it is present.

(q) The space between coracoid and cleithrum is very wide in the families Aplocheilichthyidae, Aplocheilidae and Oryziatidae; in all the other oviparous cyprinodont families it is narrow.

28. It is recommended that the fossil cyprinodonts be reexamined with special reference to such osteological characters as

the metapterygoid, the vomer, the basibranchials, the branchiostegals, the premaxillary processes, the parietals, the supraorbital processes, the exoccipital condyles, the first vertebra, the transverse processes, the prezygapophyses, and the hypurals, all of which are important in deciphering the true relationships of the fossil forms.

29. The loss of various bony elements and the modifications of others is a conspicuous feature in the evolutionary trends of the oviparous cyprinodonts.

EXPLANATION OF ABBREVIATIONS USED IN FIGURES

A	actinost
AFR	anal fin ray
AHM	articulating heads of hyomandibular
ALSPH	alisphenoid
ANG	angular
ANT	anterior
AOP	articulating head for operculum
AP	autopalatine
APLE	anterolateral process of lateral ethmoid
ART	articular
AS	asteriscus
BBR	basibranchial
BH	basihyal
BO	basioccipital
BOC	basioccipital condyle
BS	branchiostegals
BSR	branchiostegal ray
C	centrum
CA	cartilaginous area
CBR	ceratobranchial
CH	ceratohyal
CHM	concavity for hyomandibular

CL	cleithrum
CLP	cleithral process
CO	coracoid
DNT	dentary
DR	distal radial
DRS	dorsal fin rays
DSO	dome-shaped structure of supraoccipital
EAP	ethmopalatine process of autopalatine
EC	ethmoid cartilage
ELP	external lateral process
EP	epipleural
EPBR	epibranchial
EPH	epihyal
EPIO	epiotic process
EPO	epiotic
EPU	epural
EX	exoccipital
EXOC	exoccipital condyle
F	frontal
FALSPH	surface for alisphenoid
FEXC	facets for exoccipital condyle
Fig.	figure
FR	fin rays
FM	foramen magnum

HB 1	hypobranchial 1
HM	hyomandibular
HH	hypohyal
HS	haemal spine
IH	interhyal
IMX	inner process of the maxilla
IOF	interorbital portion of the frontal
IOP	interopercle
IF	interorbital portion of frontal
IPHB	inferior pharyngeal bone
ISC	impression of the semicircular canal
JF	jugular foramen
LA	lapillus
LE	lateral ethmoid
LC	lachrymal
LPHB	lower pharyngeal
MAPT	metapterygoid
MBE	membranous bony expansion
MC	meckels cartilage
ME	mesethmoid
MLE	medial portion of lateral ethmoid
MHU	median hypural
MSPT	mesopterygoid
MS	anteromesial process of the prootic

MX	. . . maxilla
N	. . . nasal
NA	. . . neural arch
NT	. . . notch
NS	. . . neural spine
OMX	. . . outer process of the maxilla
OC	. . . occipital condyle
OR	. . . orbit
OT	. . . outer teeth
P	. . . parietal
PAL	. . . palatine
PALSPH	. . . place for alisphenoid
PB	. . . pelvic bone
PBP	. . . posteriorly directed bony process
PBR	. . . pharyngobranchial
PCL	. . . postcleithrum
PHM	. . . pterotic facet for hyomandibular
PHRT	. . . pharyngeal teeth
PMX	. . . premaxilla
PMXP	. . . premaxillary process
PMY	. . . posterior myodome
PO	. . . postorbital
POP	. . . preopercle
PR	. . . proximal radials
PRO	. . . prootic

PT	. . . posttemporal
PTO	. . . pterotic
PV	. . . posterior view
PZ	. . . prezygapophyses
Q	. . . quadrate
R	. . . rib
RAP	. . . rostropalatine process of autopalatine
RID	. . . ridge
S	. . . space between cleithrum and coracoid
SA	. . . sagitta
SCA	. . . scapula
SCH	. . . sensory canal
SCL	. . . supracleithrum
SCLP	. . . sclerotic plate
SES	. . . sesamoid articular
SF	. . . sphenoidal portion of the frontal
SHM	. . . sphenotic facet for hyomandibular
SO	. . . supraoccipital
SOP	. . . suboperculum
SOPR	. . . supraoccipital process
SP	. . . space between first and second vertebrae
SPH	. . . sphenotic
SPHP	. . . sphenotic process
SPHF	. . . sphenoid portion of the frontal
SY	. . . symplectic

T	. . . teeth
TFC	. . . trigeminofacialis chamber
TLE	. . . transverse plate of lateral ethmoid
UH	. . . urohyal
US	. . . urostyle
V	. . . vomer
VLP	. . . ventrolateral process of the parasphenoid
VRT 1	. . . vertebra 1
VRT 11-13	. . vertebrae 11 through 13
VRT 14	. . . vertebra 14
VRT 15	. . . vertebra 15
VRT 23-27	. . vertebrae 23 through 27
VS	. . . vertical support
VT	. . . vomerine teeth

FIGURES

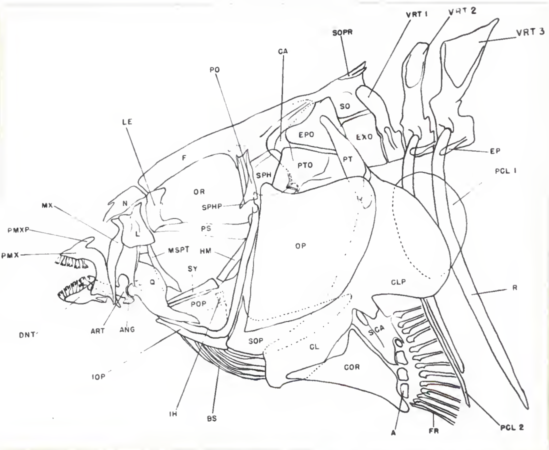


Fig. 1.--*Cyprinodon* *v.* *variegatus*: head skeleton (lateral view).

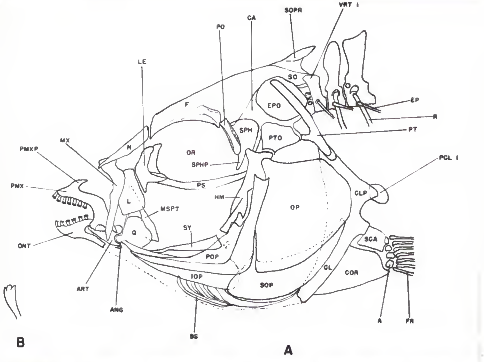


Fig. 2.--Cualac tessellatus: A, head skeleton (lateral view); B, single tooth.

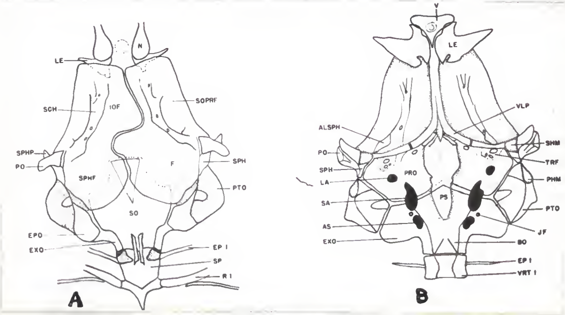


Fig. 3.--Cyprinodon v. variegatus, skull: A, dorsal view; B, ventral view.

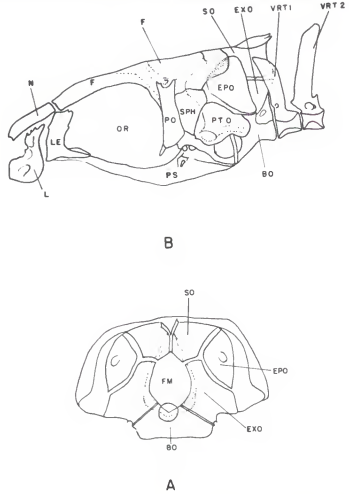


Fig. 4.--*Cyprinodon v. variegatus*, skull: A, posterior view; B, side view.

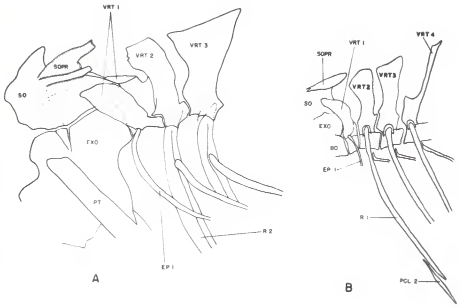


Fig. 5.--Occipital region and first three vertebrae: A, *Cyprinodon v. variegatus*; B, *Cualac tessellatus*.

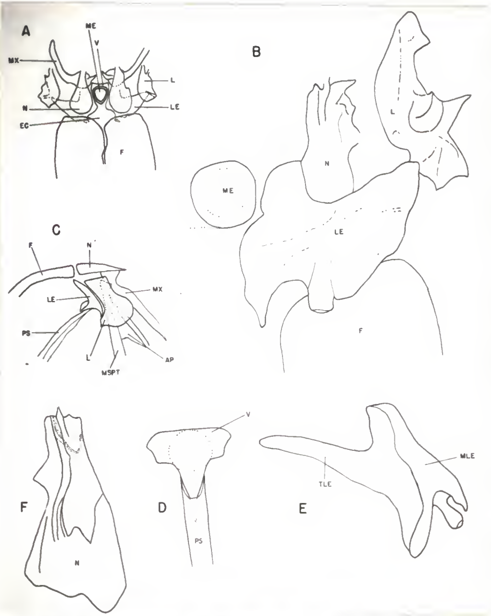


Fig. 6.--*Cyprinodon v. variegatus*: A, ethmoid region (dorsal view); B, ethmoid region (inner view); C, ethmoid region (side view); D, vomer and portion of parasphenoid (ventral view); F, nasal (dorsal view).

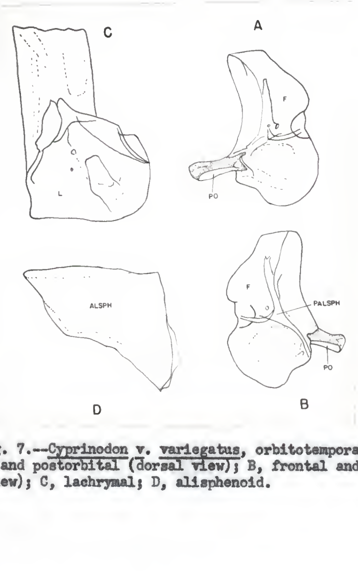


Fig. 7.--Cyprinodon v. variegatus, orbitotemporal region: A, frontal and postorbital (dorsal view); B, frontal and postorbital (ventral view); C, lachrymal; D, alisphenoid.

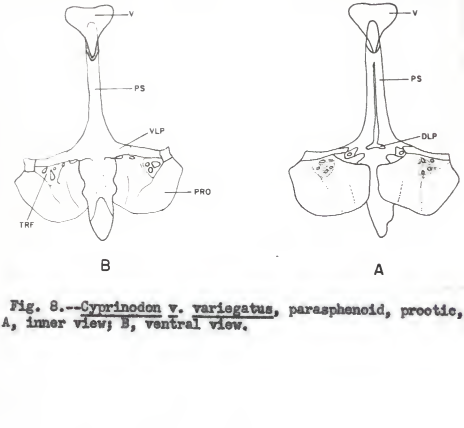


Fig. 8.--*Cyprinodon v. variegatus*, parasphenoid, prootic, and vomer: A, inner view; B, ventral view.

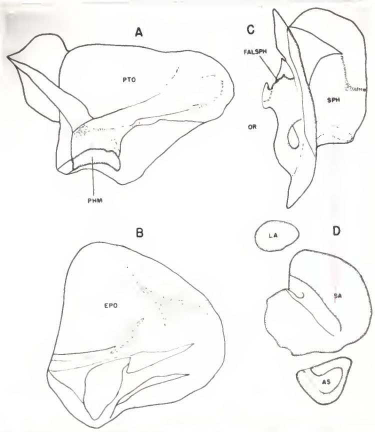


Fig. 9.--Cyprinodon v. variegatus, otic region: A, pterotic; B, epiotic; C, sphenotic; D, otoliths.

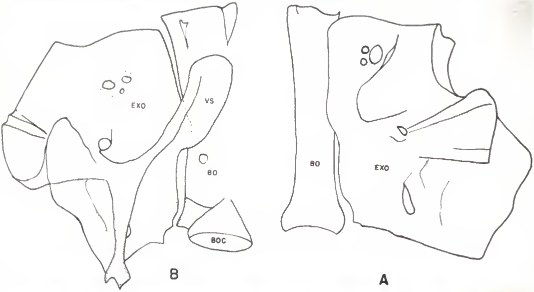


Fig. 10.--Cyprinodon v. variegatus, exoccipital and basioccipital: A, ventral view; B, inner view.

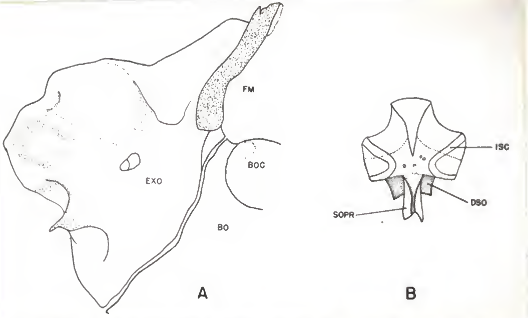


Fig. 11.--*Cyprinodon v. variegatus*: A, exoccipital and basioccipital (posterior view); B, supraoccipital (dorsal view).

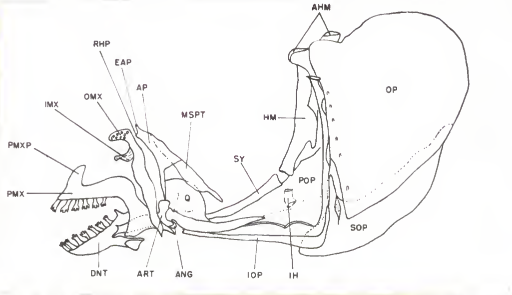


Fig. 12.--*Cyprinodon v. variegatus*: hyomandibular, symplectic, mandibular arch, and opercular bones (outer view).

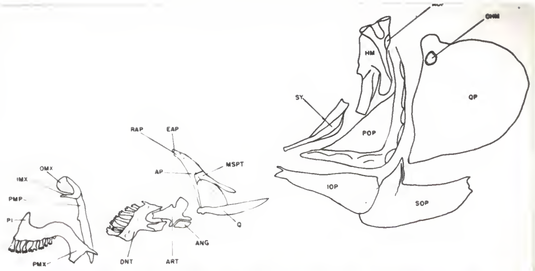


Fig. 13.--Cyprinodon v. variegatus: hyomandibular, symplectic, mandibular arch, and opercular bones (mesial view).

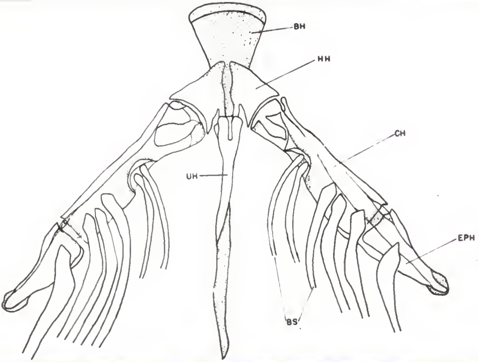


Fig. 14.--Cyprinodon v. variegatus: hyoid cornu, branchiostegals and urohyal.

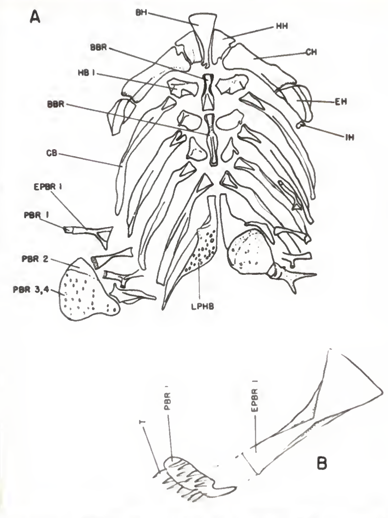


Fig. 15.--A, branchial arches of *Cyprinodon v. variegatus*; B, pharyngobranchial of *Floridichthys c. carpio*.

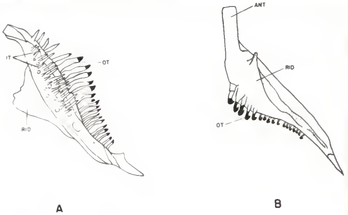


Fig. 16.--*Cyprinodon v. variegatus*, pharyngobranchials: A, inner view; B, ventral view.

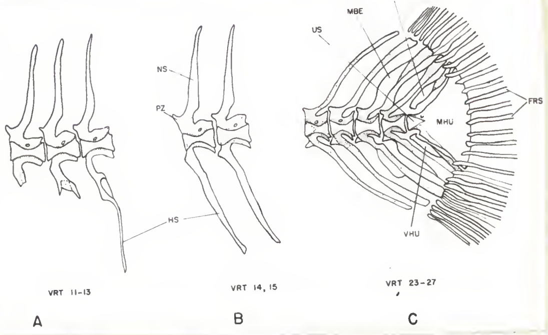


Fig. 17.--*Cyprinodon v. variegatus*: A, precaudal vertebrae; B, caudal vertebrae; C, caudal vertebrae and caudal fin.

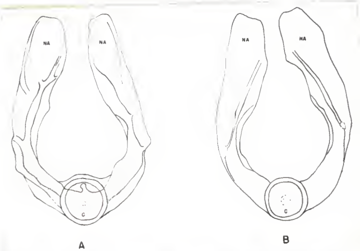


Fig. 18.--Cyrpinodon v. variegatus, first vertebra: A, anterior view; B, posterior view.

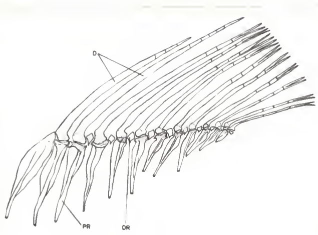


Fig. 19.--Cyprinodon v. variegatus: dorsal fin.

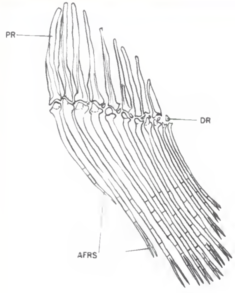


Fig. 20.--<u>Cyprinodon</u> <u>v</u>. <u>variegatus</u>: anal fin.

Fig. 21.--<u>Cyprinodon</u> <u>v</u>. <u>variegatus</u>: pelvic bones and fin rays.

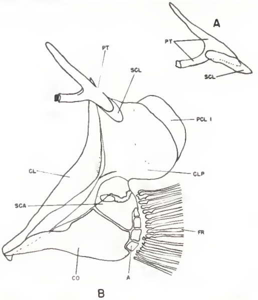


Fig. 22.—*Cyprinodon v. variegatus*: A, posttemporal and supracleithrum; B, pectoral girdle and fin rays.

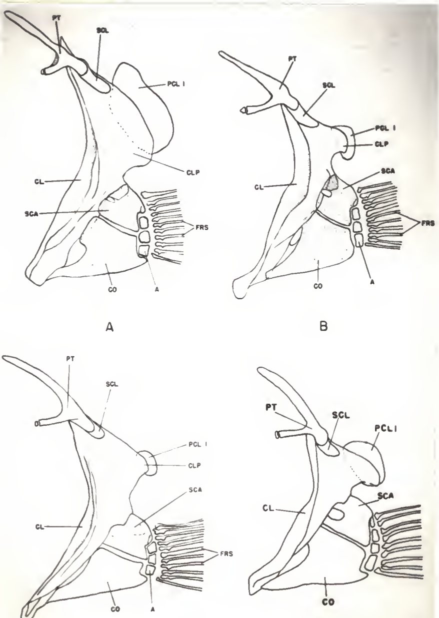


Fig. 25.--Pectoral girdle and fin rays of four species of cyprinodont fishes: A, *Jordanella floridae*; B, *Garmanella pulchra*; C, *Floridichthys c. carpio*; D, *Cualac tessellatus*.

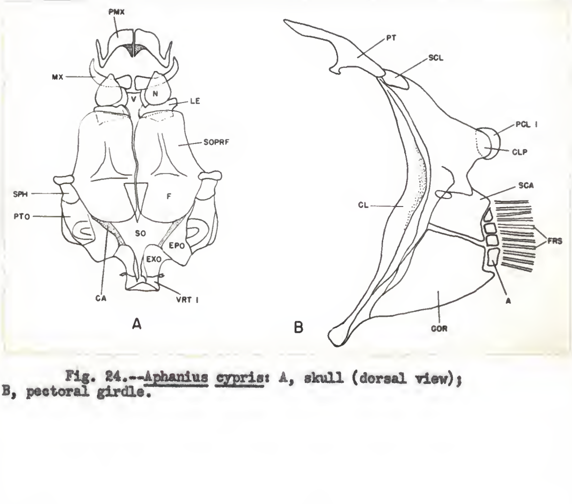


Fig. 24.--*Aphanius cypris*: A, skull (dorsal view); B, pectoral girdle.

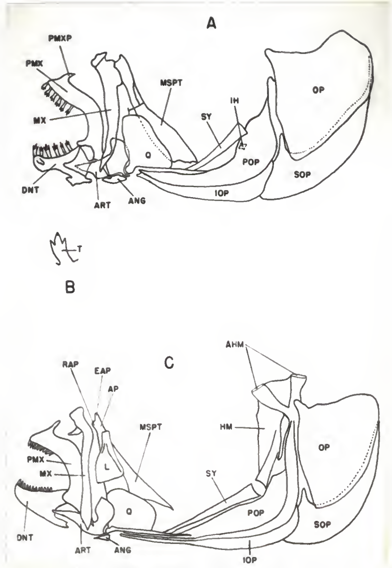


Fig. 25.--A, hyomandibular, symplectic, mandibular arch and opercular bones of *Aphanius cypris*; B, single tooth; C, hyomandibular, symplectic, mandibular arch and opercular bones of *Kosswigichthys asquamatus*.

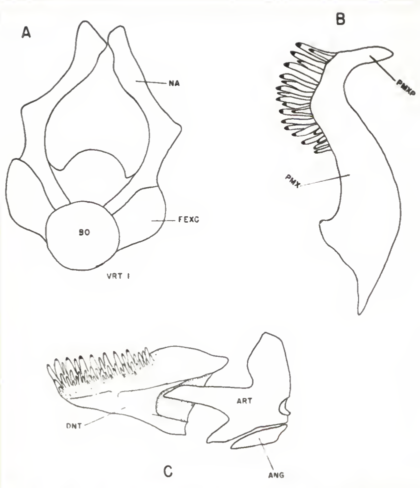


Fig. 26.--*Koswigichthys asquamatus*: A, first vertebra; B, premaxilla; C, lower jaw.

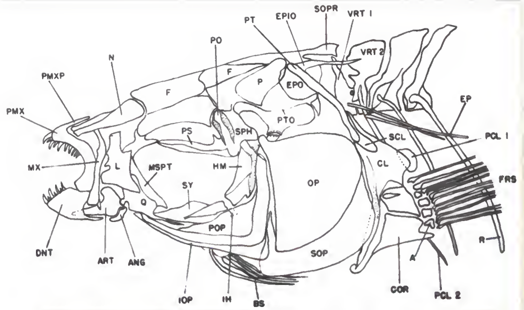


Fig. 27.--*Fundulus chrysotus*: head skeleton (lateral view).

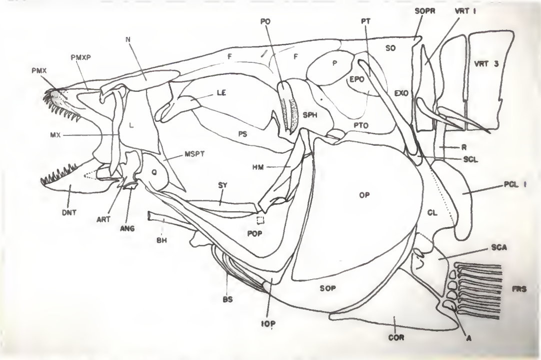


Fig. 28.--*Adinia xenia*: head skeleton.

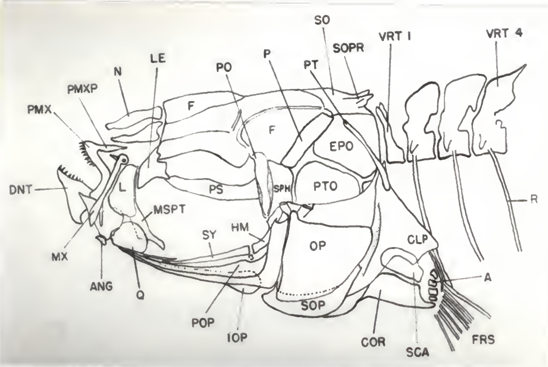


Fig. 29.--Leptolucania ommata: head skeleton (lateral view).

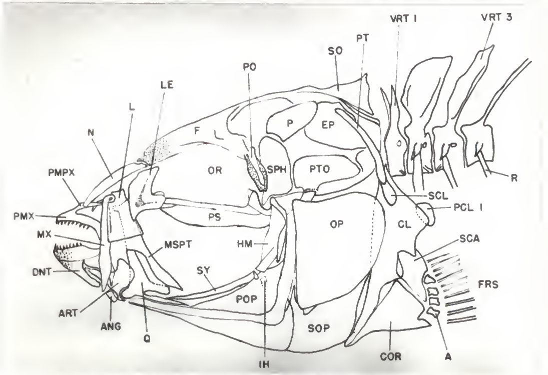


Fig. 30.--Lucania parva: head skeleton (lateral view).

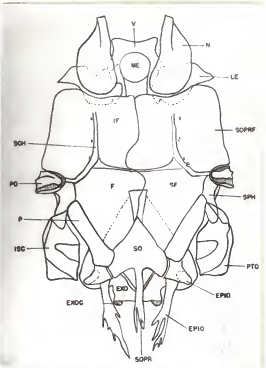


Fig. 31.--<u>Fundulus</u> <u>chrysotus</u>: skull (dorsal view).

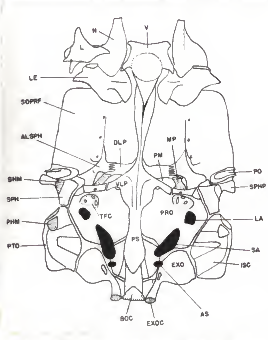


Fig. 32.--<u>Fundulus</u> <u>chrysotus</u>: skull (ventral view).

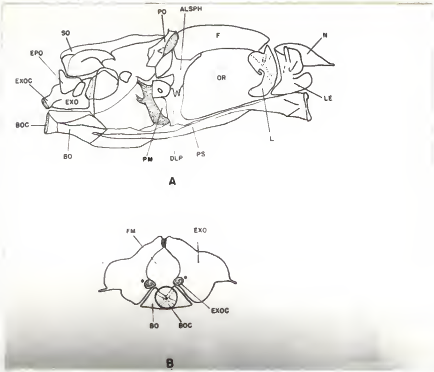


Fig. 33.--*Fundulus chrysotus*, skull: A, lateral view; B, posterior view.

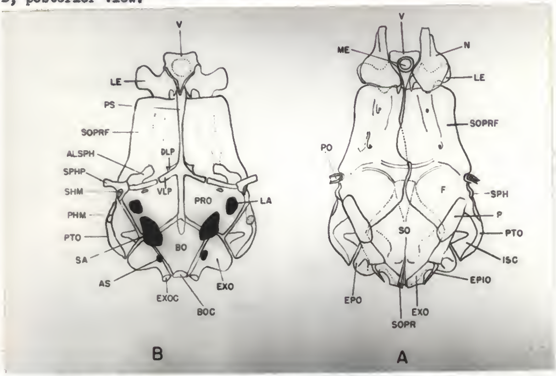


Fig. 34.--*Lucania parva*, skull: A, dorsal view; B, ventral view.

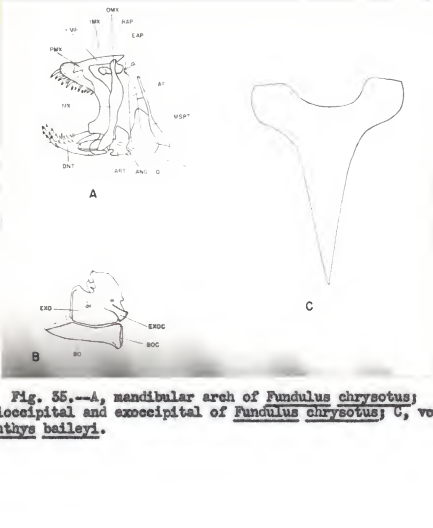


Fig. 35.--A, mandibular arch of <u>Fundulus</u> <u>chrysotus</u>; B, basioccipital and exoccipital of <u>Fundulus</u> <u>chrysotus</u>; C, vomer of <u>Crenichthys</u> <u>baileyi</u>.

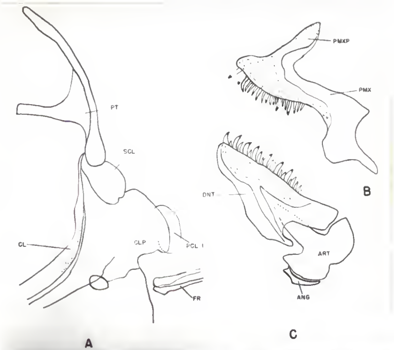


Fig. 56.--*Profundulus hildebrandi*: A, portion of pectoral girdle; B, premaxilla; C, lower jaw.

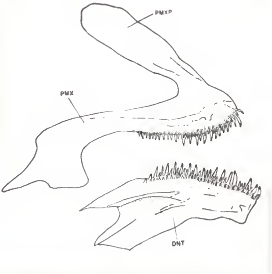


Fig. 57.--*Adinia xenica*: premaxilla and dentary.

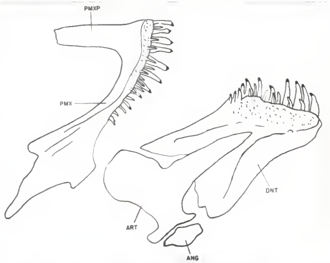


Fig. 38.--*Empetrichthys* *latos*: premaxilla and dentary.

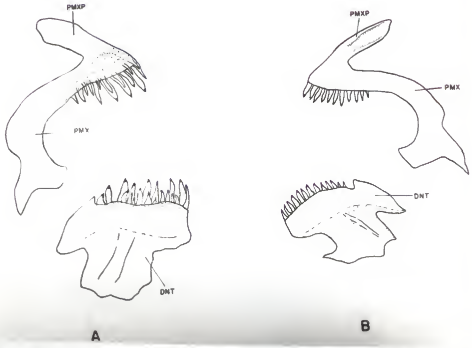


Fig. 39.--Premaxilla and dentary: A, *Chriopeops* *goodei*; B, *Lucania* *parva*.

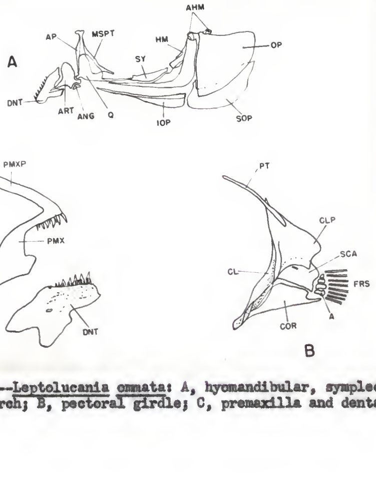


Fig. 40.--*Leptolucania ommata*: A, hyomandibular, symplectic, and mandibular arch; B, pectoral girdle; C, premaxilla and dentary.

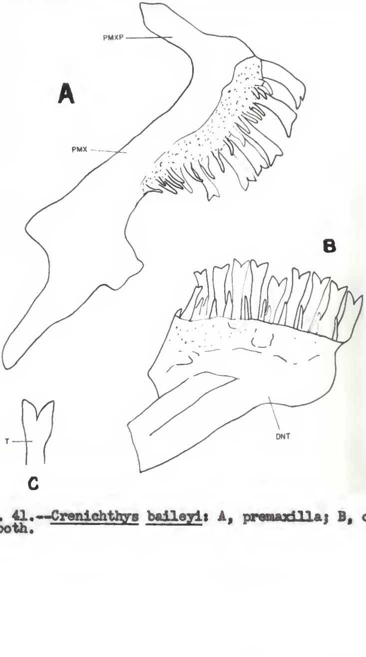


Fig. 41.--Crenichthys baileyi: A, premaxilla; B, dentary; C, single tooth.

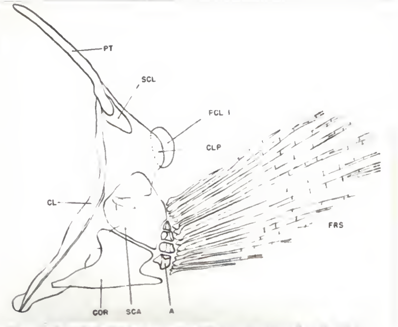


Fig. 42.--*Fundulus chrysotus*: pectoral girdle.

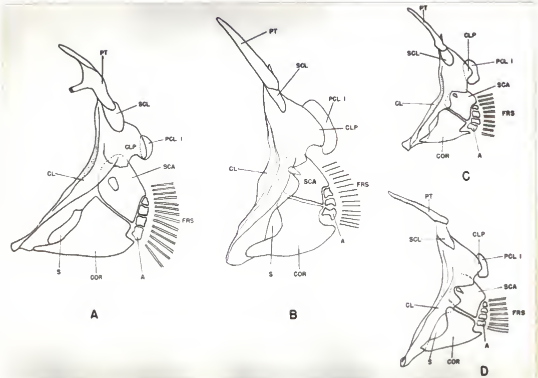


Fig. 43.--Pectoral girdle: A, *Crenichthys baileyi*; *Adinia xenica*; *Lucania parva*, and *Chriopeops goodei*.

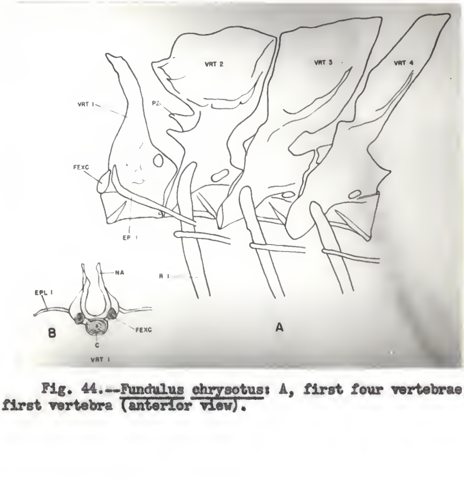


Fig. 44.--Fundulus chrysotus: A, first four vertebrae; B, first vertebra (anterior view).

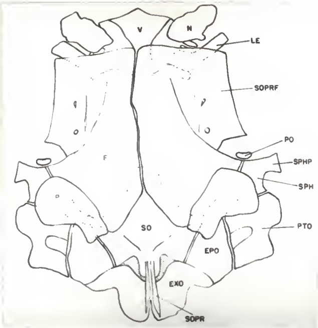


Fig. 45.--Rivulus bondi: skull (dorsal view).

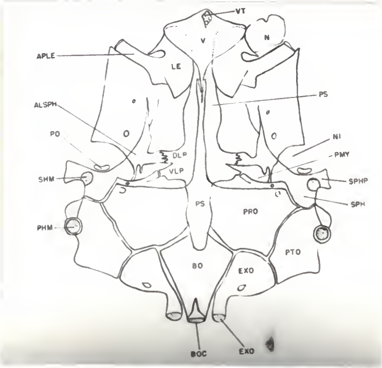


Fig. 46.--Rivulus bondi: skull (ventral view).

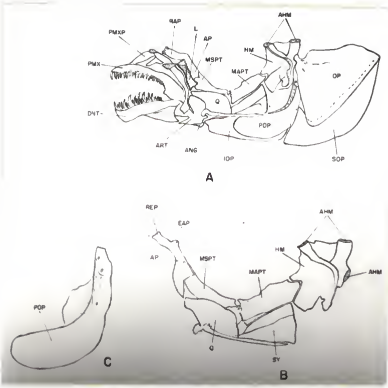


Fig. 47.--Rivulus bondi: A, hyomandibular, symplectic, mandibular arch and opercular bones; B, hyomandibular, symplectic and some bones of the mandibular arch; C, preopercle.

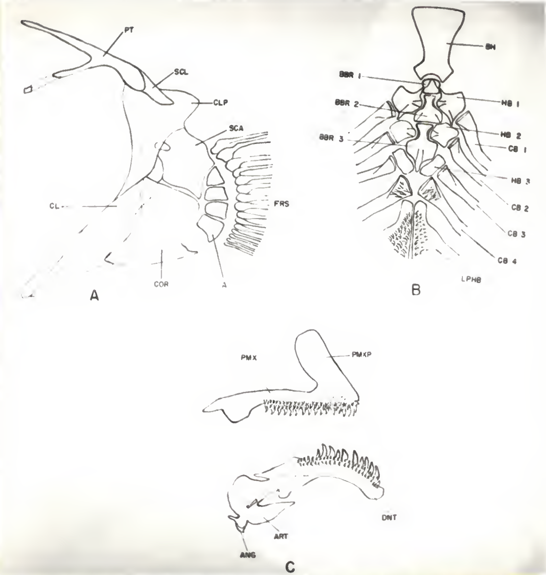


Fig. 48.--Rivulus bondi: A, pectoral girdle; B, portion of branchial skeleton; C, premaxilla and lower jaw.

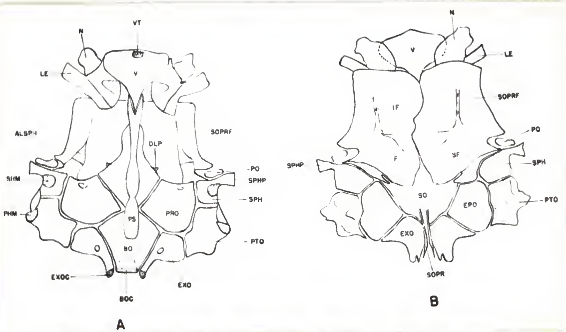


Fig. 49.--Aphyosemion caeruleum, skull: A, ventral view; B, dorsal view.

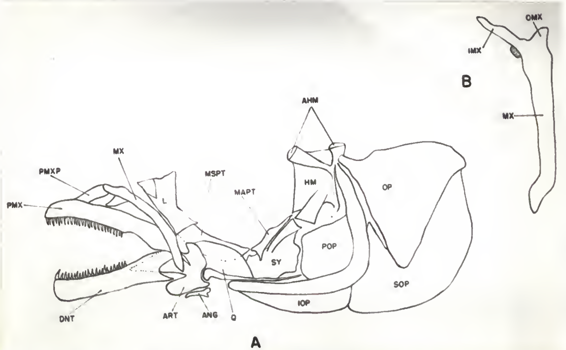


Fig. 50.--Aphyosemion caeruleum: A, hyomandibular, symplectic, mandibular arch and opercular bones; B, maxilla.

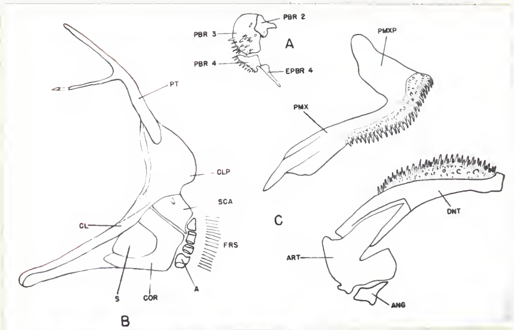


Fig. 51.--Aphyosemion caeruleum: A, pharyngobranchials; B, pectoral girdle; C, premaxilla and lower jaw.

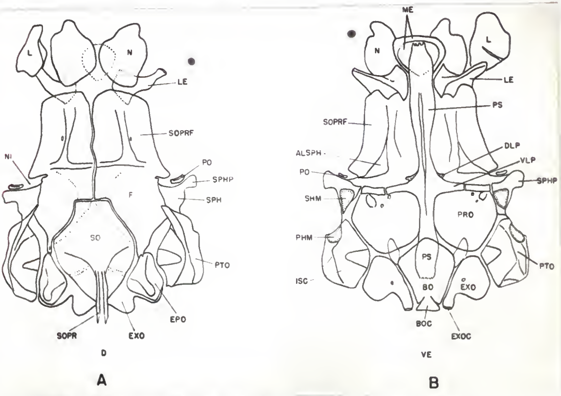


Fig. 52.--Orestias agassizii, skull: A, dorsal view; B, ventral view.

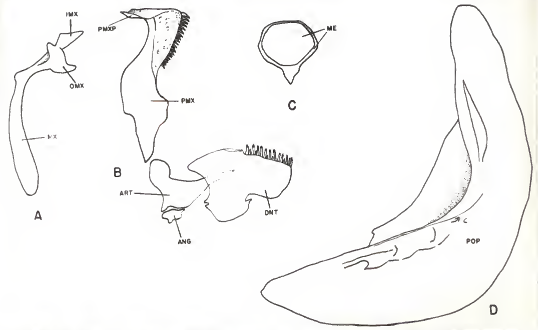


Fig. 53.--*Orestias agassizii*: A, maxilla; B, premaxilla; C, mesethmoid; D, opercle.

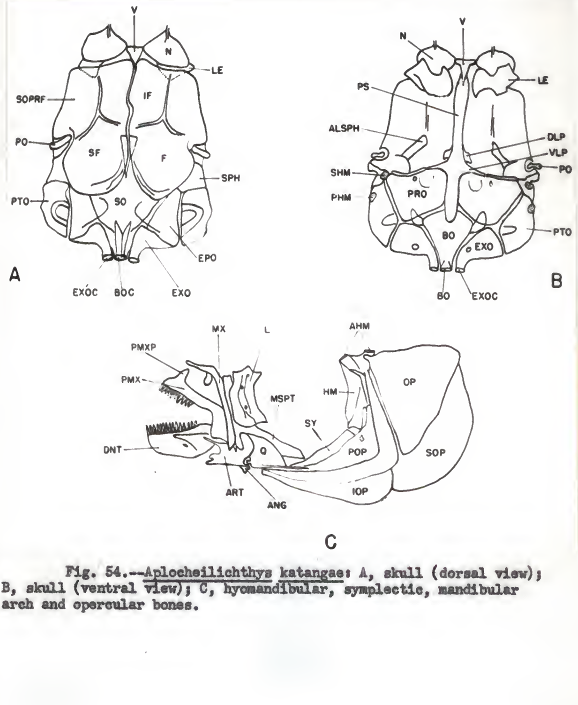


Fig. 54.--Aplocheilichthys katangae: A, skull (dorsal view); B, skull (ventral view); C, hyomandibular, symplectic, mandibular arch and opercular bones.

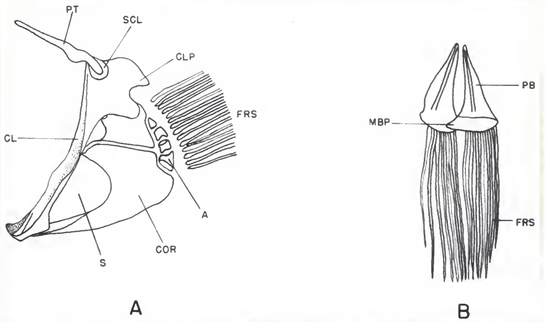


Fig. 55.--Aplocheilichthys katangae: A, pectoral girdle; B, pelvic bones and fin rays.

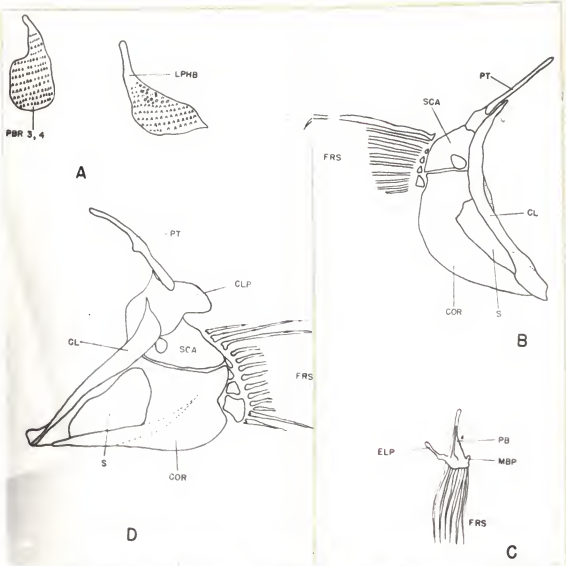


Fig. 56.--A, lower pharyngeals of Oryzias; B, pectoral girdle of Oryzias; C, pelvic bone and fin rays of Oryzias; D, pectoral girdle of Aplocheilus panchax.

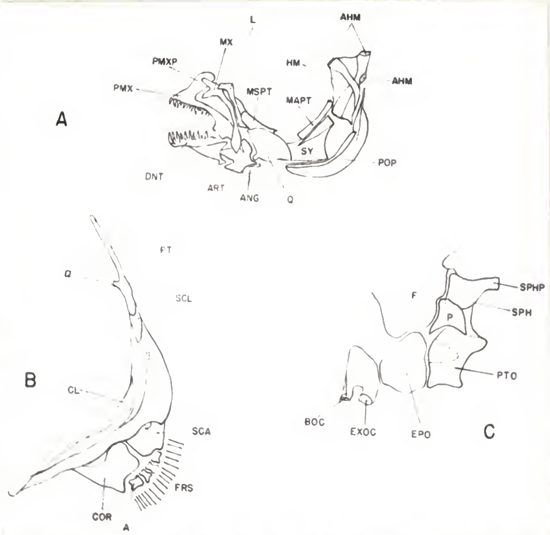


Fig. 57.--*Cynolebias whitei*: A, hyomandibular, symplectic, mandibular arch and preopercle; B, pectoral girdle; C, portion of the skull.

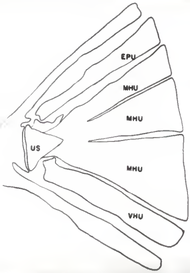


Fig. 58.--Aplocheilus panchax: trifid median hypural.

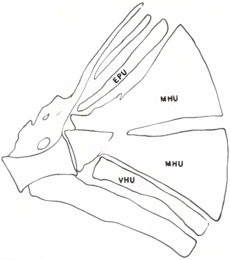


Fig. 59.--Oryzias latipes: bifid median hypural.

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BIOGRAPHICAL SKETCH

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This dissertation was prepared under the direction of the chairman of the candidate's supervisory committee and has been approved by all members of the committee. It was submitted to the Dean of the College of Arts and Sciences and to the Graduate Council and was approved as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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