

# Phylogeny and Classification of the Cyprinodontiformes (Euteleostei: Atherinomorpha): A Reappraisal

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**Abstract.** Phylogenetic relationships among cyprinodontiform families are reexamined. The analysis is based on morphology, primarily osteology, of about 250 species. It includes the 73 characters described in Parenti's (1981) phylogenetic study and 54 new characters. The strict consensus tree obtained from the three equally most parsimonious cladograms (consistency index 0.90, retention index 0.86, rescaled consistency index 0.77) has the following topology: (Rivulidae + Aplocheilidae) (Valenciidae (Cyprinodontidae (Poeciliidae + Anablepidae)) (Fundulidae (Profundulidae + Goodeidae))). Monophyly of all included families as proposed by Parenti (1981) is supported. The monophyly of Cyprinodontiformes, Aplocheiloidei, and Cyprinodontoidei is corroborated by five, nineteen and seven apomorphic conditions firstly reported herein, respectively. The present phylogenetic hypothesis differs from that of previous morphological studies, but is similar to a recent molecular phylogeny in the proposed sister group relationships between Profundulidae and Goodeidae, and between the clade consisting of those families and the Fundulidae. The monophyly of the clade comprising Fundulidae, Profundulidae and Goodeidae (Funduloidea, new usage) is supported by a reduced dorsal process of the maxilla, ventrally curved distal portion of the ventral maxillary process, and an anteriorly expanded mesethmoidal region. The monophyly of the clade composed of the Cyprinodontidae, Poeciliidae and Anablepidae (Cyprinodontoidea, new usage) is supported by a broad, rounded dorsal process of the maxilla, a short premaxillary ascending process, an elongate dorsomedial process of the autopalatine, the posteriorly bent dorsal tip of the dorsal process of urohyal, and medially expanded nasals.

**Resumo.** As relações filogenéticas entre as famílias de Cyprinodontiformes são reexaminadas. A análise é baseada na morfologia, principalmente osteologia, de cerca de 250 espécies. São incluídos 73 caracteres descritos no estudo filogenético de Parenti (1981) e 54 caracteres novos. A árvore de consenso estrito obtida dos três cladogramas igualmente mais parcimoniosos (índice de consistência 0,90, índice de retenção 0,86, índice de consistência reescalado 0,77) apresenta a seguinte topologia: (Rivulidae + Aplocheilidae) (Valenciidae (Cyprinodontidae (Poeciliidae + Anablepidae)) (Fundulidae (Profundulidae + Goodeidae))). O monofiletismo de Cyprinodontiformes, Aplocheiloidei e Cyprinodontoidei é respectivamente corroborado por cinco, dezenove e sete condições apomórficas registradas pela primeira vez. A presente hipótese filogenética difere daquelas propostas em estudos morfodgicos anteriores, mas é semelhante a uma recente filogenia molecular, na relação de grupos-irmãos proposta entre Profundulidae e Goodeidae, e entre este clado e Fundulidae. O monofiletismo do clado compreendendo Fundulidae, Profundulidae e Goodeidae (Funduloidea, novo uso), é sustentado por processo dorsal de maxila reduzido, porção distal de processo ventral de maxila ventralmente curvo e região mesetmoidal expandida anteriormente. O monofiletismo do clado englobando Cyprinodontidae, Poeciliidae e Anablepidae (Cyprinodontoidea, novo uso) é sustentado pelo processo dorsal da maxila largo e arredondado, processo ascendente da pré-maxila curto e nasais medialmente expandidos.

## Introduction

The order Cyprinodontiformes comprises the most speciose assemblage of atherinomorph fishes, including approximately 850 species in about 110 genera. It is currently classified into two suborders, Aplocheiloidei and Cyprinodontoidei, encompassing two and seven families, respectively (Parenti, 1981). Whereas the Aplocheiloidei includes nearly 380 species, widely distributed in tropical America, Africa, and southern Asia, the Cyprinodontoidei occurs in North, Middle, and South America, Africa, and the coastal plains and river basins around the Mediterranean, Black, Red, and Arabian seas. Cyprinodontiform fishes are most abundant and often the predominant fish group in some tropical areas, but are particularly diverse in Middle America, where about one third of all known species occur, representing seven families. They usually inhabit shallow freshwater biotopes or brackish coastal habitats, in several environments, including rain forests and deserts, commonly at sea level, but sometimes at altitudes over 4000m.

Usually small, about three to five centimeters in total length, and with attractive color patterns, many cyprinodontiform species are popular aquarium fishes. A combination of easy maintenance in captivity, and interesting features, such as complex behaviors, chromatic polymorphism, hermaphroditism, and unique life cycles, make cyprinodontiforms important experimental animals. However, despite broad scientific interest in these fishes, little progress was made in elucidating the phylogenetic relationships within the order until relatively recently. Old classifications used artificial criteria to separate families, based primarily on the occurrence of viviparity and associated structures. Thus, the cyprinodontiforms were divided into a large oviparous family, Cyprinodontidae, and three or four viviparous families, Goodeidae, Poeciliidae, Anablepidae, and Jenynsiidae (e.g. Hubbs, 1924; Myers, 1931). This classificatory scheme was drastically altered by the classification proposed by Parenti (1981), based on a phylogenetic analysis primarily based on osteological features. The Cyprinodontidae was dismantled and the members were either placed in their own families, or placed within each of the remaining four families with viviparous taxa, with a total of nine cyprinodontiform families recognized. For a historical review of classification of cyprinodontiform fishes see Garman (1895) and Parenti (1981).

The classification proposed by Parenti (1981) has been widely adopted and promulgated in textbooks up to the present time (e.g. Nelson, 1994; Moyle & Cech, 1996; Helfman *et al.*, 1997). However, despite some phylogenetic studies on Neotropical taxa (e.g., Parenti, 1984; Costa, 1990a, 1996, 1997; Ghedotti, this volume), involving the families Rivulidae, Poeciliidae, Anablepidae, and Cyprinodontidae, and debates on the phylogeny of atherinomorph orders (e.g. Stiassny, 1990; Parenti, 1993), the relationships between cyprinodontiform families, as proposed by Parenti (1981), have not been reexamined in a morphological context. However, a molecular phylogeny (Meyer & Lydeard, 1993), based

on a few representatives of most cyprinodontiform lineages supported a distinct hypothesis of familial relationships, which was reinforced by a combined analysis of available morphological and molecular data by Parker (1997). Relationships between some cyprinodontiform families also have been tested through molecular techniques (Grant & Riddle, 1995; Murphy & Collier, 1997). On the other hand, seventeen years have passed since the publication of Parenti's phylogenetic analysis, a period in which many new taxa were described and some groups intensively studied. Hence, the aim of this present study is to test current phylogenetic hypotheses of the Cyprinodontiformes through the analysis of new osteological characters and a reevaluation of characters used in previous morphological studies.

## Materials and Methods

Cladistic methodology was used to erect a hypothesis of relationships. Most parsimonious cladograms were obtained using the implicit enumeration command of the program Hennig86 (Farris, 1988). Outgroups include species of the two other orders of Atherinomorpha (Beloniformes and Atheriniformes). Character state polarization was made using multiple out-groups (Maddison *et al.*, 1984) according to current hypotheses on Atherinomorpha relationships (e.g. Rosen & Parenti, 1981; Dyer & Chernoff, 1996), in which cyprinodontiforms are more closely related to beloniforms than to atheriniforms. However, since many structures are highly modified in beloniforms, polarization was largely based on diverse atheriniform taxa. Recent hypotheses on relationships of atheriniform taxa were used as a basis to infer basal conditions within this clade (Dyer & Chernoff, 1996; Aarn & Ivantsoff, 1997). Character state determinations for outgroups were augmented with data and illustrations of non-cyprinodontiform atherinomorph taxa available in Rosen (1964), Rosen & Parenti (1981), White (1985), Chernoff (1986), Ivantsoff *et al.* (1987), Stiassny (1990), Dyer & Chernoff (1996), and Aarn & Ivantsoff (1997). In order to not unnecessarily expand the data matrix, the out-group is represented by a single line with all character states coded 0, what is consistently employed for all characters. The nine families (Aplocheilidae, Rivulidae, Profundulidae, Fundulidae, Valenciidae, Poeciliidae, Anablepidae, Goodeidae and Cyprinodontidae) as defined by Parenti (1981) were the terminal taxa. In cases where evidence of the basal condition for a given character in polymorphic terminal taxa is absent, characters were coded as unknown. All character states of multistate characters were treated as unordered.

Material examined is listed in the Appendix A. Osteological preparations were made following the method of Taylor & Van Dyke (1985). Osteological nomenclature is that of Weitzman (1962), with modifications as described in Vari (1989). Nomenclature for musculature follows Winterbottom (1974), for sensory canals of the head follows Gosline (1949), and for frontal squamation follows Hoedeman (1956).

### Character analysis

To describe and discuss characters, they are grouped into two categories. The first one, termed “informative characters,” includes characters with states consistently distributed among the proposed terminal taxa. Characters of this category are further grouped into subcategories, according to the region in which morphological structures are located. Characters used in previous studies as well as states first recorded herein are included in this category. Characters widely discussed in previous phylogenetic studies, when consistent with the present analysis, are only briefly described herein, followed by references to previous discussions and illustrations. The distribution of character states for each terminal taxon is presented in the data matrix of Appendix B. The second category, termed “non-informative characters,” includes all characters used in previous studies, but not found to have derived states consistent with the terminal taxa herein analyzed.

#### Informative characters

##### Jaws

(1) Size of the dorsal process of maxilla. State 0: long, medially directed, approximately parallel to ventral process; state 1: short, anteriorly directed, not parallel to ventral process; state 2: vestigial. Parenti (1981) judged an enlarged dorsal process of the maxilla to be an apomorphic condition shared by valenciids, poeciliids, anablepids, goodeids, and cyprinodontids. She recognized a medially expanded dorsal process of the maxilla as being further derived in cyprinodontids and expanded medially (Figs. 1G-H). Thus, Parenti (1981) considered the short process of the maxilla in profundulids and fundulids to be plesiomorphic. However, a long dorsal process occurs in all basal atherinomorph groups (Fig. 1A), thus this character is herein considered plesiomorphic for the order. In addition, Parenti (1981) reported a greatly reduced dorsal process as secondarily reduced and apomorphic for goodeids (Fig. 1F). Parenti (1981) also considered an elongate and attenuate dorsal process to be synapomorphic for valenciids, but the condition is indistinguishable from that observed in outgroups to Cyprinodontiformes. Therefore, the greatly reduced dorsal process of maxilla in fundulids, profundulids, and goodeids is apomorphic (Figs. 1D-F). Furthermore, the dorsal process of aplocheiloids is distinct in being both short and anteriorly-directed (Figs. 1B-C), hence consisting of a distinct character state.

(2) Shape of the dorsal process of maxilla. State 0: narrow; state 1: broad. Parenti (1981), recognized a clade comprising anablepids, poeciliids, goodeids, and cyprinodontids that is diagnosed by a rounded or greatly reduced dorsal maxillary process. The rounded process, better defined as a broad process (Figs. 1G-H), occurs in anablepids, poeciliids, and cyprinodontids, whereas a greatly reduced process occurs in all goodeids (Fig. 1F). Since there is no evidence to interpret the broad and the reduced conditions as the same character transformation series, they are separately analyzed (see character 1 above). Furthermore, the reduced condition of goodeids is not

distinct from that of fundulids and profundulids. The broad dorsal maxillary process of anablepids, poeciliids, and cyprinodontids is, in contrast, unique among cyprinodontiforms and other atherinomorph taxa. However, the comparison of this character (narrow or broad process) is not pertinent to those taxa with a minute dorsal maxillary process (goodeids, profundulids, and fundulids), and the character is coded as “?” for them in the data matrix.

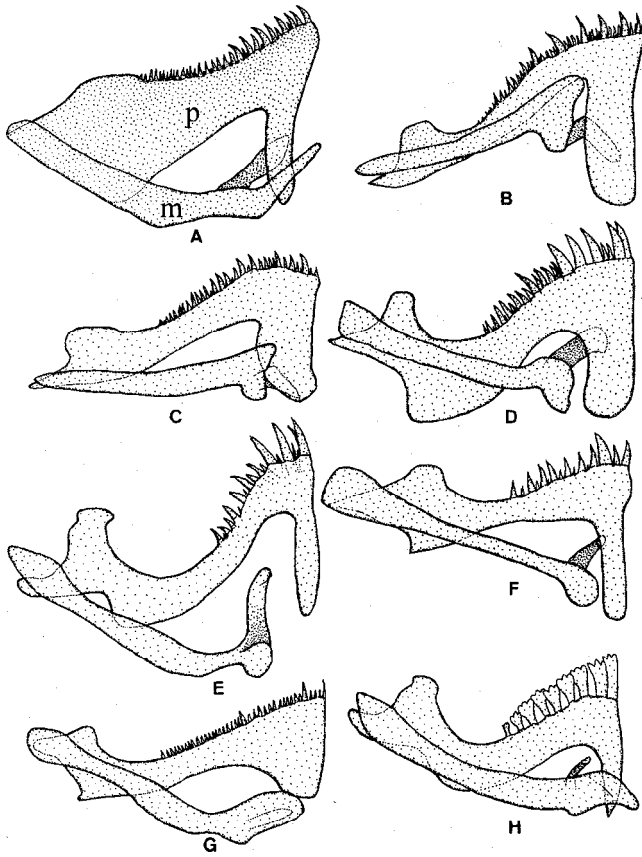
(3) A distinct groove on the dorsal process of maxilla. State 0: absent; state 1: present. Among other derived features, Parenti (1981) diagnosed cyprinodontids by having the dorsal process of the maxilla medially expanded and possessing a distinct groove (Fig. 1H). This is corroborated in the present analysis.

(4) Shape and orientation of the main axis of the ventral process of maxilla. State 0: approximately straight, directed anteromedially; state 1: slightly curved, tip directed posteriorly; state 2: bent and directed posteriorly, median portion expanded anteriorly, producing a triangular shape. Parenti (1981) described a triangular flange on the anterior face of the ventral process of the maxilla as synapomorphic for rivulids. This corresponds to character state 2 which is herein interpreted as a bent ventral process (Fig. 1B). Aplocheilids, however, have an intermediate condition, in which the ventral process of the maxilla is also directed posteriorly, but only slightly curved (Fig. 1C). In other atherinomorphs, including cyprinodontoids, the ventral process is never directed posteriorly (Figs. 1D-H). In fundulids, the main axis of the process is directed anteriorly, which is considered a distinct apomorphic condition, as discussed below (Fig. 1E).

(5) Size and orientation of the main axis of the ventral process of the maxilla. State 0: length moderate, directed anteromedially; state 1: long, directed anteriorly. The apomorphic condition of an anteriorly directed ventral process of the maxilla in fundulids, as described by Parenti (1981) (Fig. 1E), is corroborated. However, the pronounced hooks, also described as synapomorphic for fundulids, are herein interpreted to have a process with a ventrally curved distal tip, thus being homologous to the similar condition in profundulids and goodeids (see character 7 below).

(6) Shape of the distal arm of the maxilla. State 0: narrow to slightly widened; state 1: distinctively widened. As discussed and illustrated by Parenti (1981), the distal arm of the maxilla of poeciliids and anablepids is widened. Whereas most aplocheiloids have a narrow distal arm (Figs. 1B-C), cyprinodontoids usually have a robust arm (Figs. 1D-F, H). However, in poeciliids and anablepids the distal portion undergoes an anterior expansion medially preceded by a constriction, forming a markedly widened distal section (Fig. 1G).

(7) Shape of the distal tip of the ventral process of the maxilla. State 0: continuous to the main axis of the distal portion of the process; state 1: abruptly curved ventrally. The distal-most portion of the ventral maxillary process of profundulids, fundulids, and some goodeids is curved, its tip being ventrally-directed (Fig. 1E). This condition, noteworthy in the fundulids, *Profundulus guatemalensis*, *P. labialis*, and in the goodeid genus *Crenichthys*, is only slightly visible in the



**Figure 1.** Left premaxilla (p) and maxilla (m), dorsal view, of: **A**, *Atherinella brasiliensis*; **B**, *Rivulus brasiliensis*; **C**, *Nothobranchius rachovii*; **D**, *Profundulus guatemalensis*; **E**, *Lucania goodei*; **F**, *Empetrichthys latos*; **G**, *Alfaro huberi*; and **H**, *Garmanella pulchra*.

goodeid genus *Empetrichthys* and *Profundulus candalarius*, and is absent in the Goodeinae in which the ventral process is atrophied. As discussed above, this apomorphic condition corresponds to the pronounced hooks described by Parenti (1981) for fundulids.

(8) Ethmomaxillary ligament. State 0: present; state 1: absent. As discussed by Parenti (1981) this ligament is present in primitive atherinomorphs and aplocheiloids. Therefore, its absence is considered apomorphic for cyprinodontoids.

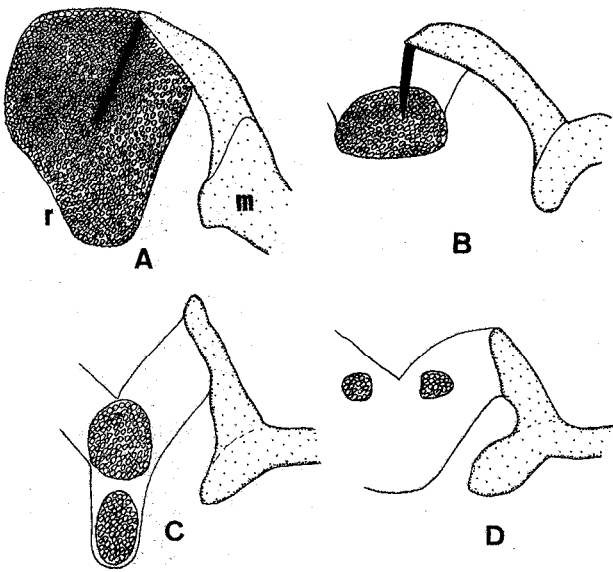
(9) Size of the rostral cartilage and ligament between the ventral process of maxilla and the middle of the rostral cartilage. State 0: rostral cartilage large and ligaments well-developed; state 1: rostral cartilage small or absent, ligaments absent, rostral cartilage when present embedded in thickened and elongate connective tissue between ventral processes of maxilla; state 2: rostral cartilage minute or absent, ligaments absent, thin connective tissue between ventral processes. Parenti (1981) distinguished two states of rostral cartilage size in cyprinodontiforms: large in aplocheiloids and profundulids, and reduced or absent in the remaining taxa. She considered the absence of rostral ligaments as a distinct character state,

occurring in all the cyprinodontoids. However, these ligaments are always present when the rostral cartilage is well-developed (Fig. 2A), occurring in all profundulids examined (Fig. 2B). Therefore, the reduction of the rostral cartilage is associated with the loss of middle ligaments, and is thus interpreted as a single character state. In the same way, the possession of inner arms of the maxillaries that do not abut the rostral cartilage (Parenti, 1981) is not independent of the reduced rostral cartilage. When the rostral cartilage is reduced but not absent, there are two different conditions for the connective tissue between ventral processes: thick, as occurring in fundulids and goodeids with a rostral cartilage (*Empetrichthys* and *Crenichthys*), and thin, as in valenciids, poeciliids, anablepids, and cyprinodontids.

(10) Meniscus between the ventral process of the maxilla and the ascending process of the premaxilla. State 0: present; state 1: absent. The derived absence of a meniscus between the maxilla and the premaxilla in the cyprinodontoids, reported by Parenti (1981), is confirmed.

(11) Shape of the rostral cartilage. State 0: rounded; state 1: transversely elongate. Atherinomorphs other than cyprinodontiforms typically have a rounded rostral cartilage, similar to that occurring in most aplocheiloids, except in several members of the Rivulidae that have a longitudinally elongate cartilage (Fig. 2A). In cyprinodontoids, with a few exceptions, the cartilage is rounded, even in groups where it is reduced. Profundulids, however, possess a transversely elongate rostral cartilage (Fig. 2B) which is slightly smaller than those of outgroups, but larger than those of other cyprinodontoids (see character 9). In goodeids the rostral cartilage is present only in *Crenichthys* and *Empetrichthys*. In *Crenichthys* the rostral cartilage, although reduced, is very similar in shape to that of profundulids. *Empetrichthys*, however, has a unique morphology of the rostral cartilage, consisting of two small cartilage discs transversely arranged (Fig. 2D) that is herein interpreted as a derived division of the former transversely elongate cartilage. Therefore, since the apomorphic condition occurs in all examined profundulids and goodeids with a rostral cartilage, the character is coded as apomorphic for the two families. Another modified rostral cartilage is found in the anablepid genus *Anableps* which has a diagnostic dumbbell-shaped cartilage (Parenti, 1981), a distinct derived condition.

(12) Small cartilage posterior to the rostral cartilage (accessory rostral cartilage). State 0: absent; state 1: present. Alexander (1967) described the rostral cartilage of *Fundulus* as Y-shaped, but as discussed by Parenti (1981) the use of specific techniques for staining cartilages not available at that time demonstrated that the rostral cartilage of *Fundulus* and closely related genera is rounded (Fig. 2C). The equivocal condition described by Alexander was due to the dense rostral connective tissue of fundulids and some other cyprinodontoid taxa (see character 9) that is Y-shaped in fundulids. However, Parenti (1981) reported that the rostral cartilage of fundulids is composed of four small cartilaginous discs. In fact, fundulids have a rostral cartilage approximately in the same position as in other cyprinodontiforms, but possessing an



**Figure 2.** Ventral process of left maxilla (m) and rostral cartilage (r), ventral view, of: A, *Pterolebias obliquos*; B, *Profundulus guatemalensis*; C, *Fundulus majalis*; and D, *Empetrichthys latos*.

additional posterior small cartilage (Fig. 2C), herein termed the accessory rostral cartilage, a unique apomorphic condition.

(13) A distinct anterior expansion of the alveolar arm of premaxilla. State 0: absent; state 1: present. Atherinomorphs have a robust alveolar arm of the premaxilla (Fig. 1A) without a distinct anterior expansion distally that follows a proximal, concave anterior border, as observed in all cyprinodontiforms (Figs. 1B-H). This condition has also been described as a two-part alveolar process (Alexander, 1967), and is synapomorphic for cyprinodontiforms (Parenti, 1981).

(14) Posterior indentation of the alveolar arm of premaxilla. State 0: absent; state 1: present. As described by Parenti (1981), cyprinodontoids have an S-shaped alveolar arm formed by the strong indentation in its posterior border (Figs. 1D-H), rather than the straight or convex border of aplocheiloids and remaining atherinomorphs (Figs. 1A-C). Parenti (1981) also described a reversed straight alveolar arm in goodeids but this condition could not be confirmed (Fig. 1F).

(15) Shape of the posterior tip of the ascending process of premaxilla. State 0: not curved medially; state 1: curved medially. Parenti (1981) described a posteriorly tapering premaxillary ascending process as synapomorphic for aplocheilids. The apomorphic condition of the ascending process of aplocheilids is herein interpreted as a medially curved posterior tip, forming a concavity on its posteromedial edge (Fig. 1C), and constituting a shape unique among cyprinodontiforms.

(16) Size of the premaxillary ascending process. State 0: long; state 1: shortened. Parenti (1981) recognized three patterns of ascending processes in cyprinodontiforms: flat and broad in aplocheiloids and fundulids, long and narrow in fundulids,

short and pointed or triangular in valenciids, poeciliids, anablepids, and cyprinodontids. In the same study, the elongate ascending processes of fundulids and valenciids were considered plesiomorphic when compared with the short and narrow processes of anablepids, poeciliids, goodeids, and cyprinodontids. This classification of ascending processes is thus derived from a combination of four different parameters: width (broad or narrow), thickness (flat), length (long or short), and shape (pointed or triangular). These conditions are in fact more variable in cyprinodontiforms and outgroups than indicated by these groupings. The ascending process of aplocheiloids and profundulids are as flat as any other cyprinodontiform and their outgroups. Variation in width is approximately the same in most cyprinodontiforms and outgroups, but distinctively broader in some poeciliids, aplocheilids, and anablepids as discussed below (character 18). In fundulids the processes are elongate, in keeping with the elongation of the entire premaxilla which is considered a distinct apomorphic condition (character 17 below). A triangular or pointed shape was observed only in some cyprinodontid taxa (Fig. 1H) and *Crenichthys*. It thus is not considered diagnostic for any family or assemblage of terminal taxa in the present analysis. Similarly, some reduction in width seems to be associated with extreme reduction in length in goodeines and some cyprinodontids. However, some reduction in the length of the ascending process compared with the variability recorded in most outgroup taxa is, in part, consistent with Parenti's analysis. The ascending process is evidently reduced in poeciliids, anablepids, and cyprinodontids (Figs. 1G-H). In goodeids, it is not reduced in *Empetrichthys* (Fig. 1F), slightly reduced in *Crenichthys*, and vestigial in goodeines. Thus, the condition is coded as polymorphic for this family in the data matrix.

(17) Shape of the premaxilla. State 0: robust; state 1: elongate. The premaxilla of atherinomorphs is typically robust, a condition more obvious in most cyprinodontoids because of their apomorphically wide, sinuous alveolar arm (Fig. 1D). In fundulids, however, the entire premaxilla is elongate with a consequently long anterior process of the alveolar arm and a lengthened ascending process (Fig. 1E).

(18) Shape of the premaxillary ascending process. State 0: not widened; state 1: widened. Non-cyprinodontiform atherinomorphs usually have the ascending process of moderate to somewhat narrow width (Fig. 1A). Except for an aplocheilid clade with a distinctly pointed snout and a few rivulids, aplocheiloids lack a wide ascending process (Figs. 1B-C). Most cyprinodontoids have a condition that approximates the condition in most outgroup taxa, both with and without a reduced ascending process (Figs. 1D, F, H). In contrast, poeciliids and anablepids have a widened ascending process, typically only slightly separated from the posterior border of the bone by the reduction of a concavity at the angle between the ascending process and the main arm of the bone (Fig. 1G; see also Parenti, 1981, fig. 35B, for an illustration of the premaxilla of the anablepid genus *Oxyzygonectes*). The derived widened condition is absent in a poeciliine clade defined by,

among other apomorphic features, a very reduced ascending process (Costa, 1991) as well as in *Anableps* that lacks such a process (Parenti, 1981). That condition is not very clear in the anablepid genus *Jenynsia*, which has a wide basal portion, but with the process tapered posteriorly.

(19) Shape of the dentary. State 0: slender; state 1: deep. The dentary of the cyprinodontoids, as described by Parenti (1981) is expanded vertically to form a robust lower jaw (Figs. 3B, C), rather than being elongate as in aplocheiloids and most atherinomorphs (Fig. 3A).

(20) Reduction of the posteroventral process of the dentary. State 0: not reduced; state 1: reduced. Most atherinomorphs have a pronounced posteroventral process of the dentary, a condition more conspicuous in the majority of cyprinodontoids because of their derived robust jaw. Anablepids and poeciliids, however, have a reduced posteroventral process (Fig. 3B).

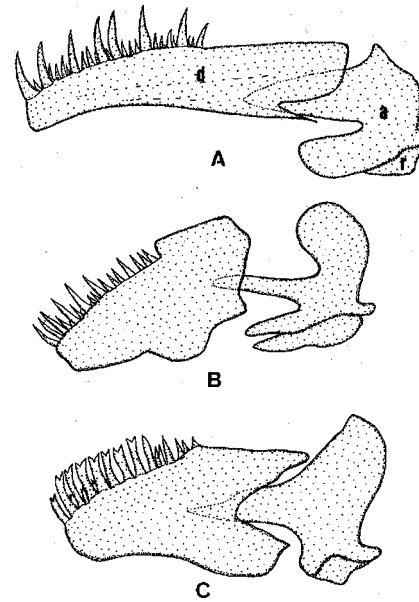
(21) Shape of the retroarticular and ventral process of the anguloarticular. State 0: short; state 1: long. Parenti (1981) described an extremely elongate retroarticular as synapomorphic for anablepids and poeciliids. The lengthened retroarticular in those taxa is paralleled by a long ventral process of the anguloarticular, which reaches a vertical just posterior to the anterior tip of the median process, producing a peculiar shape of the anguloarticular (Fig. 3B). In other cyprinodontiforms, the tip of the median process lies along a vertical much anterior to the anterior tip of the ventral process (Figs. 3A, C).

(22) Shape of the ventral process of the anguloarticular. State 0: not expanded; state 1: expanded. Aplocheilids have a distinctive, transversely expanded ventral process of the anguloarticular (Fig. 3A). A similar apomorphic condition is also present in a sister pair of species in the rivulid genus *Rivulus* (Costa, 1990b) and in *Profundulus guatemalensis*. These are considered to be independent acquisitions.

(23) Reduction of the coronoid process of anguloarticular. State 0: not reduced; state 1: reduced. A prominent coronoid process occurs in most atherinomorphs, including cyprinodontoids (Figs. 3B, C). In aplocheiloids the coronoid process is represented by a weak dorsal expansion of the anguloarticular (Fig. 3A).

(24) A pronounced indentation on the anterior base of the coronoid process of anguloarticular. State 0: absent; state 1: present. Poeciliids exhibit the derived presence of a pronounced indentation on the anterobasal angle of the coronoid process of the anguloarticular (Fig. 3B), rather than the slight concavity which occurs in other atherinomorphs (Figs. 3A, C).

(25) Shape of teeth. State 0: conical; state 1: tricuspid. As discussed by Parenti (1981), anablepids differ from most other atherinomorphs in having tricuspid teeth. A similar tooth morphology occurs in a cyprinodontid clade defined by Costa (1997) and the named Cyprinodontini. However, the hypothesized basal condition for the Cyprinodontidae is the conical tooth form (Costa, 1997) therefore coded as "0" in the data matrix. A bifid tooth morphology is present in several goodeid taxa, but the condition is considered unrelated to the one described above.



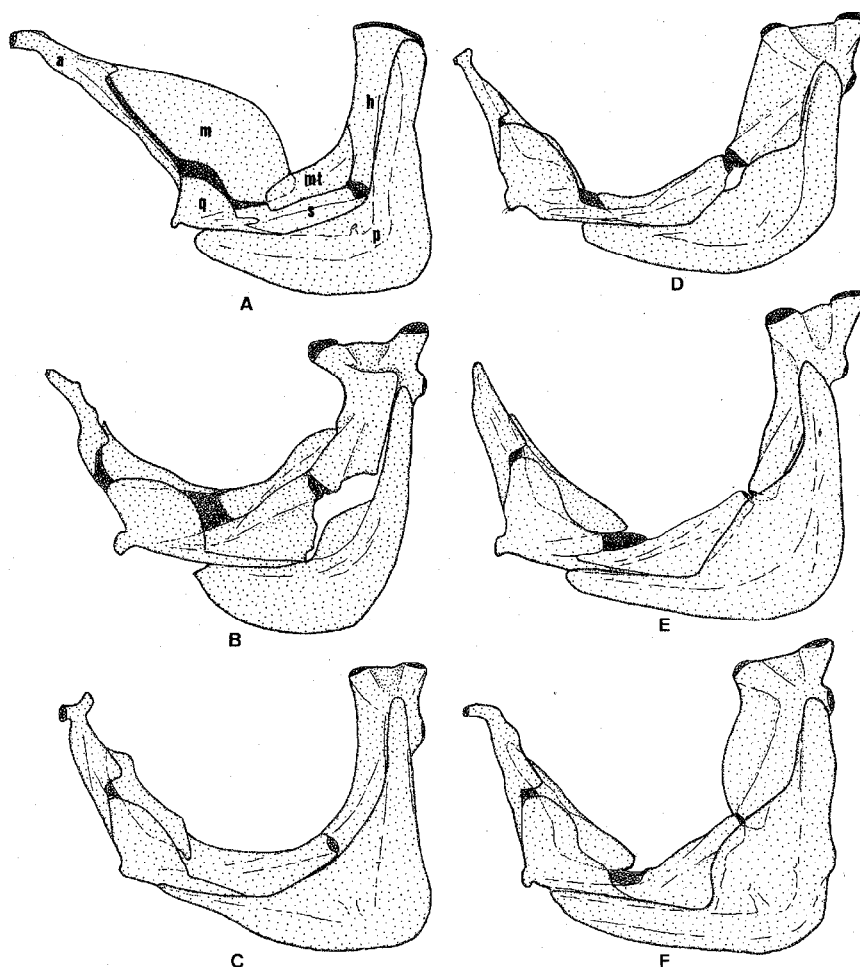
**Figure 3.** Left dentary (d), anguloarticular (a), and retroarticular (r), lateral view, of: **A**, *Aphyosemion cameronense*; **B**, *Aplocheilichthys hutereaui*; and **C**, *Crenichthys baileyi*.

(26) Tendon of the superficial (A1) division of *adductor mandibulae* attached to lacrimal. State 0: present; state 1: absent. As discussed by Stiassny (1990) and Parenti (1993) the loss of such a tendon, present in other atherinomorphs, is an apomorphic condition shared by cyprinodontiforms.

#### Jaw suspensorium and opercular apparatus

(27) Position and shape of the head of the autopalatine. State 0: slightly curved anteriorly, continuous with the main longitudinal axis of the bone; state 1: bent anteriorly, displaced laterally relative to the main axis of the bone. Parenti (1981) cited a sharply bent and hammer-shaped anterior extension of the autopalatine as synapomorphic for cyprinodontoids. The anteriorly bent autopalatine head (Figs. 4C, D) is confirmed as apomorphic to that clade, although not conspicuously apparent in most goodeids (Fig. 4E), which have the dorsal portion of autopalatine reduced (see character 30). In aplocheiloids and other atherinomorphs the dorsal tip of the autopalatine is only slightly curved anteriorly (Figs. 4A, B). Comparisons with outgroups to cyprinodontiforms indicate that cyprinodontoids possess a further modification of the autopalatine head, consisting of a lateral displacement relative to the main axis of the bone. The hammer shape described by Parenti (1981), which results from a posteriorly extended bony flange, is not common to all cyprinodontoids and is herein considered a distinct character (character 29).

(28) Extent of the ventral portion of the autopalatine. State 0: long, overlapping upper portion of quadrate; state 1: short, not contacting quadrate. Parenti (1981) considered a long ventral extension of the autopalatine, covering part of the quadrate as a synapomorphy of cyprinodontoids. However, the ventral extension of the autopalatine is as long in cyprinodontoids



**Figure 4.** Left jaw suspensorium, lateral view, of: **A**, *Melanotaenia* sp.; **B**, *Neofundulus paraguayensis*; **C**, *Procatopus noto-taenia*; **D**, *Valencia hispanica*; **E**, *Girardinichthys multiradiatus*; and **F**, *Profundulus guatemalensis*. Abbreviations: a, autopalatine; h, hyomandibula; m, mesopterygoid; mt, metapterygoid; p, preopercle; q, quadrate; and s, symplectic. Dots indicate bone, and circles cartilage.

(Figs. 4C-F) as in aplocheilids and other atherinomorph groups (Fig. 4A). Therefore, the reduced ventral extension of the autopalatine of rivulids (Fig. 4B) is coded as apomorphic. (29) Extent and shape of the dorsomedial flange of the autopalatine. State 0: a short, indistinct flange; state 1: a prominent flange, sometimes forming a short process; state 2: a distinctive elongate process. Parenti (1981) described a hammer shaped autopalatine with a posterior bony flange on its dorsal tip as synapomorphic for cyprinodontoids. However, the condition is not shared by all members of the Cyprinodontidae and, when present, depending on the size of the process, may be classified as two separate character states. Profundulids and goodeids lack the dorsomedial expansion of the autopalatine (Figs. 4E, F) found in other atherinomorph groups (Figs. 4A, B). Fundulids and valenciids have a pronounced osseous flange (Fig. 4D) or a small process in some species of *Fundulus*, which corresponds to state 1 above. Anablepids, most aplocheilichthyine poeciliids, and cyprinodontids have a distinct elongate process which corresponds to state 2 (Fig. 4C). Because a part of the Poeciliidae (poecili-

ines) lacks expansions or processes on the dorsomedial region of the autopalatine the character is coded as polymorphic for this family. The cyprinodontid genus *Orestias*, which has an apomorphically reduced dorsal portion of autopalatine (Costa, 1997), lacks any bony extension in that region. However, due to the presence of an elongate process both in *Cubanichthys*, the sister group of the remaining cyprinodontids, and in all other cyprinodontids, the basal condition for the Cyprinodontidae is inferred to be character state 2.

(30) Reduction of the cartilaginous head of the autopalatine. State 0: not reduced; state 1: reduced. As reported by Parenti (1981), the head of the autopalatine is reduced in goodeids (Fig. 4E). Uyeno & Miller (1962) described the autopalatine as reduced in *Empetrichthys* and *Crenichthys*, although not so reduced in *Empetrichthys merriami*. The autopalatine cartilage in these taxa is reduced to a minute, almost imperceptible point. Another reduction of the autopalatine, but a not similar condition, occurs in the cyprinodontid genus *Orestias* (Costa, 1997), in which the entire dorsal portion of autopalatine is strongly narrowed.

(31) Shape of the cartilaginous head of the autopalatine. State 0: narrow; state 1: wide. The head of the palatine of most cyprinodontiforms and outgroups is slightly narrow. Poeciliids, in contrast, possess a relatively wide cartilage head (Fig. 4C)

(32) Reduction of the dorsal edge of the mesopterygoid. State 0: expanded to the infraorbital region; state 1: reduced to a thin laminar bone. Atherinomorphs typically have a robust mesopterygoid which is medially expanded to form the base of the orbit (Rosen, 1964) (Fig. 4A). All cyprinodontiforms, in contrast, possess a reduced mesopterygoid that carries a distinctive dorsolateral fold (Figs. 4B-F) which is more conspicuous in cyprinodontoid taxa. A reduced mesopterygoid also occurs in phallostethid atheriniforms and adrianichthyoid beloniforms (Rosen, 1964), but is not the basal condition for these taxa.

(33) Concavity on the posterior margin of the quadrate. State 0: absent; state 1: present. The quadrate of profundulids and goodeids differs from those of other atherinomorphs in having a distinct concavity on its posterior margin (Figs. 4E, F). In aplocheiloids this margin is convex and in other cyprinodontoids, it is convex or approximately straight (Figs. 4 A-D). Only in the goodeid genus *Empetrichthys* is such a concavity absent.

(34) Metapterygoid. State 0: present; state 1: absent. As discussed by Parenti (1981), the loss of the metapterygoid is an unambiguous apomorphic condition uniquely shared by the Cyprinodontoidei.

(35) Extent of the lateral flange of the hyomandibula. State 0: short; state 1: expanded dorsoposteriorly. Cyprinodontoids, like most other atherinomorphs, have a short lateral flange parallel to and attached to the dorsal arm of the preopercle (Figs. 4C-F). Aplocheiloids, in contrast, have the dorsal portion of this rim expanded posteriorly and overlapping the anterior edge of the opercle (Fig. 4B).

(36) Reduction of the preopercle. State 0: preopercle robust, L-shaped, with an expanded anterior rim and well-developed sensory canal; state 1: preopercle thin, C-shaped, with a reduced median rim and vestigial sensory canal. Parenti (1981) cited the weakly-developed preopercular sensory canal of rivulids as synapomorphic. Subsequently, Costa (1990a) added an apomorphic C-shaped preopercle with a reduced anterior rim to the diagnosis of the family (Fig. 4B).

#### Hyoid arch

(37) Shape of the urohyal. State 0: slender; state 1: deep. Atherinomorphs typically have a slender urohyal (Fig. 5A). In cyprinodontiforms, the urohyal is clearly deeper (Figs. 5B-D), although very variable in shape.

(38) Dorsal process of the urohyal. State 0: well-developed; state 1: vestigial or absent. The urohyal of cyprinodontiforms has a distinct dorsal process (Figs. 5B, D), a condition that occurs in some other atherinomorphs. This process may be vestigial in some species of *Fundulus*, but it is absent in the majority of fundulids (Fig. 5C).

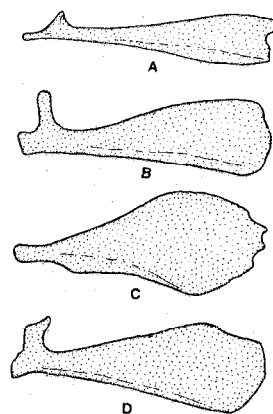
(39) Shape of the dorsal process of the urohyal. State 0:

straight; state 1: bent posteriorly. The urohyal of most cyprinodontiforms, including aplocheiloids, valenciids, profundulids, and goodeids, bears an approximately straight dorsal process (Fig. 5B), a condition similar to that exhibited by outgroups. In anablepids, poeciliids, and cyprinodontids this dorsal process is bent posteriorly, usually forming a distinct expanded anterodorsal surface (Fig. 5D). Among poeciliids, this condition is conspicuous in aplocheilichthyines and gambusin poeciliines. In the putative plesiomorphic poeciliine genus *Tomeurus*, which has a modified urohyal, the dorsal process is slightly bent on its base. In Alfaro, the process is very reduced and bent. In most other poeciliines the dorsal process is very narrow and straight, the primitive condition. However, since the apomorphic condition occurs in aplocheilichthyines and basal groups of poeciliines, the character is coded as polymorphic for this family. The character is coded as unknown for fundulids which lack such a urohyal process (see character 38).

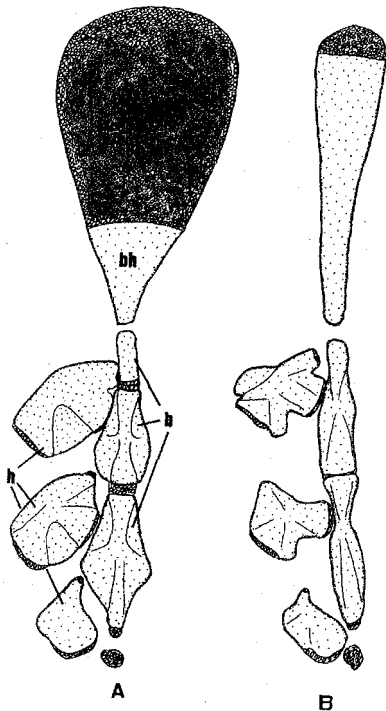
(40) Position and shape of the ventrolateral flange of the urohyal. State 0: perpendicular to the main axis of the urohyal; state 1: expanded ventrally. The urohyal of the cyprinodontiforms and most other atherinomorphs has a ventrolateral flange approximately positioned at an angle of 90° relative to the main axis of the bone and producing an inverted T-shape when viewed posteriorly. In contrast, the urohyal flange of valenciids is lateroventrally directed, producing a Y-shape when viewed posteriorly.

(41) Dorsal hypohyal. State 0: present; state 1: absent. As discussed and illustrated by Parenti (1981, fig. 28), cyprinodontoids uniquely share a derived absence of the dorsal hypohyal.

(42) Condyles on the anterior portion of the anterior ceratohyal. State 0: two distinct condyles; state 1: a single terminal condyle. As discussed and illustrated by Parenti (1981, fig. 28), the plesiomorphic condition of the anterior ceratohyal in cyprinodontiforms is the presence of two distinct condyles connected to hypohyal cartilages, even when the dorsal hypohyal is absent. Poeciliids, in contrast, possess an unbranched anterior tip to the anterior ceratohyal.



**Figure 5.** Urohyal, left lateral view, of **A**, *Melanotaenia* sp.; **B**, *Neofundulus paraguayensis*; **C**, *Fundulus majalis*; and **D**, *Cyprinodon variegatus*.



**Figure 6.** Basihyal (bh), basibranchials (b) and left hypobranchials (h), dorsal view, of: **A**, *Aplocheilus wernerii*; and **B**, *Lucania goodei*. Dots indicate bone, and circles cartilage.

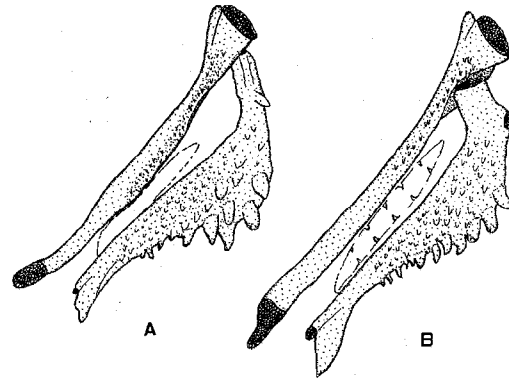
(43) Shape of the basihyal. State 0: slender; state 1: anterior portion widened. A synapomorphic broad anterior end of basihyal (Fig. 6A) is diagnostic for the Aplocheiloidei according to Parenti (1981), a condition confirmed in the present study. A reversal among rivulids occur in the annual fish tribe Plesiolebiatini (Costa, 1995a).

(44) Basihyal cartilage. State 0: larger than osseous portion; state 1: reduced, restricted to anterior part of basihyal. Parenti (1981) described the markedly reduced bony portion of basihyal (Fig. 6A) as synapomorphic for aplocheilids. However, since an expanded cartilaginous portion of basihyal occurs in all atherinomorph outgroup taxa, this condition is considered plesiomorphic. Therefore, reduction of the basihyal cartilage is considered apomorphic for rivulids and cyprinodontoids.

#### Branchial arch

(45) First basibranchial. State 0: present; state 1: absent. The presence of two instead of three basibranchials considered to be synapomorphic for cyprinodontoids by Parenti (1981) is confirmed (Fig. 6B).

(46) A distinct anteromedial process on the second hypobranchial, oriented towards the second basibranchial. State 0: absent; state 1: present. The second hypobranchial of cyprinodontoids and other non-aplocheiloids atherinomorphs has a medial articular cartilaginous surface directed to the third basibranchial (Fig. 6B). In aplocheiloids there is an additional, small articular cartilaginous surface oriented towards the second basibranchial (Fig. 6A).



**Figure 7.** Left fourth and fifth ceratobranchials, dorsal view, of: **A**, *Neofundulus paraguayensis*; and **B**, *Valencia hispanica*. Dots indicate bone, and circles cartilage.

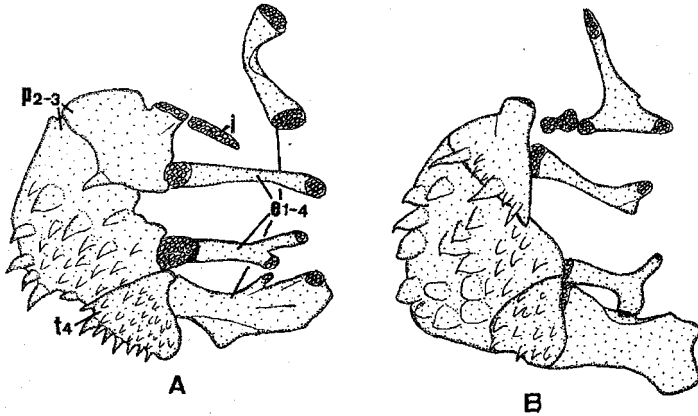
(47) A distinct, anteriorly expanded rim on the anterior border of the first hypobranchial. State 0: absent; state 1: present. Fundulids uniquely have this anterior expansion of the first hypobranchial (compare the plesiomorphic condition for cyprinodontiforms in Fig. 6A with the apomorphic condition shared by fundulids in Fig. 6B).

(48) Extent and shape of the ventral process of the fourth ceratobranchial. State 0: short; state 1: expanded medially. In aplocheiloids and most other atherinomorphs there is a short ventral process on the fourth ceratobranchial, which is not easily seen in a dorsal view of the gill arches (Fig. 7A). The anterior tip of the fifth ceratobranchial does not reach a vertical through any portion of the fourth ceratobranchial, or sometimes ventrally overlaps the anterior portion of that bone. The fourth ceratobranchial of cyprinodontoids has a medially expanded ventral process which is readily visible in dorsal view (Fig. 7B). Consequently, the anterior portion of the fifth ceratobranchial lies dorsal to that process. The ventral process of the fourth ceratobranchial is absent in the cyprinodontid clade termed the Cyprinodontini (Costa, 1997), and is very reduced or absent in goodeines. This is considered a reversal in the Cyprinodontini, since basal cyprinodontid taxa retain the condition described for all cyprinodontoids, but is coded as polymorphic for goodeids.

(49) Reduction of the anterior cartilage head of the fifth ceratobranchial. State 0: not reduced; state 1: narrow and reduced. This cartilage is very reduced in aplocheiloids (Fig. 7A), contrary to other atherinomorphs that have a well-developed cartilage head on the anterior tip of the fifth ceratobranchial (Fig. 7B).

(50) Teeth on posterior half of third ceratobranchial. State 0: absent; state 1: present. Fundulids are unique among cyprinodontiforms and other atherinomorphs examined by having teeth on the posterior half of the dorsal surface of the third ceratobranchial.

(51) Cartilage between medial margins of the fifth ceratobranchials. State 0: absent; state 1: present. Valenciids are unique among cyprinodontiforms in possessing a ball of cartilage uniting the medial margins of the fifth ceratobranchials (Fig. 7B).



**Figure 8.** Left dorsal gill arches, ventral view, of: **A**, *Maratecoara lacortei*; and **B**, *Crenichthys baileyi*. Abbreviations: e, epibranchials 1-4; i, interarcual cartilage; p2-3, pharyngobranchials 2-3; and t4, tooth-plate of pharyngobranchial 4. Dots indicate bone, and circles cartilage.

(52) Reduction of the membrane aperture between the fourth and fifth ceratobranchials. State 0: not reduced; state 1: reduced. The branchial aperture between the fourth and fifth ceratobranchials of atherinomorphs is plesiomorphically a wide aperture, approximately occupying all the space between those ceratobranchials, and with several gill rakers along its borders (Fig. 7B). In aplocheiloids this aperture is reduced by the expansion of the membrane and the adjacent gill rakers are very reduced or, more commonly, absent (Fig. 7A).

(53) Number of gill rakers on the anterior arm of the first arch. State 0: usually seven to 12; state 1: 13 to 23. As discussed by Parenti (1981), profundulids have 14 to 23 gill rakers on the anterior arm of the first arch whereas other cyprinodontiforms usually have seven to 12. High numbers of gill rakers are also present in all anablepids (Ghedotti, pers. comm.), and are occasionally found in a few members of other cyprinodontiform families (e.g. the goodeid *Crenichthys*, the valenciid *Valencia*, and the cyprinodontids *Garrmanella*, *Cyprinodon*, and *Orestias*).

(54) Shape of the ventral portion of the first epibranchial. State 0: moderately wide; state 1: very wide. The ventral end of the first epibranchial of goodeids is unique among cyprinodontiforms in being extremely expanded, usually forming two separate cartilage heads (Fig. 8B).

(55) A ventral process on the lateral portion of the second epibranchial. State 0: present; state 1: absent. Atherinomorphs other than cyprinodontiforms usually have a distinct ventral process on the lateral tip of second epibranchial which has a ligament uniting it to third ceratobranchial (Fig. 8B). Among the cyprinodontiforms this putative plesiomorphic condition is found only in aplocheiloids, profundulids, and goodeids, since such a process is absent in all other cyprinodontiform taxa analyzed (Fig. 8A).

(56) Reduction of the uncinata process of the third epibranchial. State 0: not reduced; state 1: reduced. The plesiomorphic condition of the third epibranchial for atherinomorphs is the presence of an elongate uncinata process (Fig. 8B), which is present in most cyprinodontiforms. Rivulids, in contrast, have a very reduced uncinata process (Fig. 8A).

(57) A distinct posterior process on the fourth epibranchial. State 0: absent; state 1: present. Aplocheiloids uniquely among cyprinodontiforms possess a distinct process on the posterior border of the fourth epibranchial (Fig. 8A).

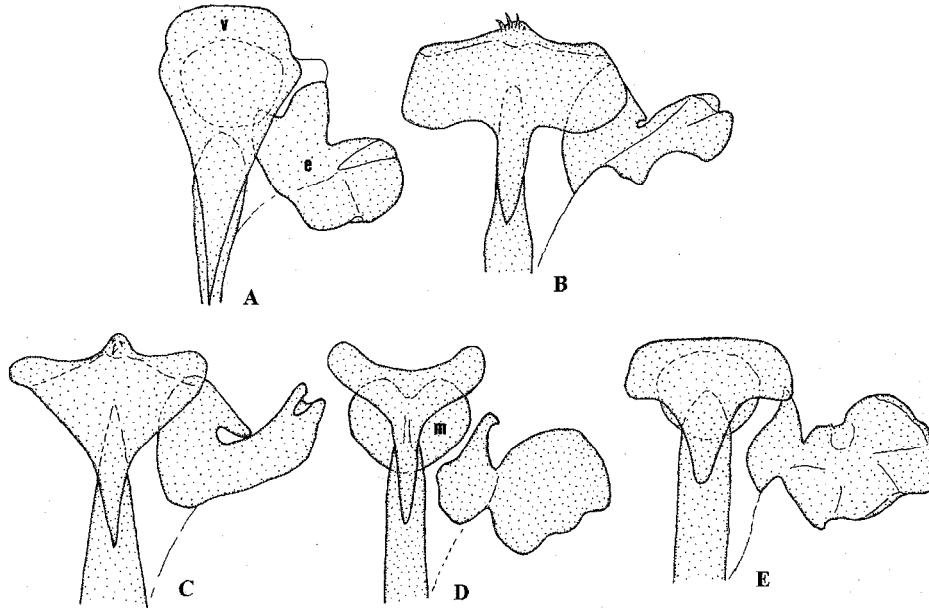
(58) Extent of the second pharyngobranchial. State 0: not expanded; state 1: expanded ventrally. Uniquely among cyprinodontiforms and other atherinomorphs examined, the posterolateral corner of the second pharyngobranchial of the cyprinodontoids is expanded ventrally to form a pointed extension (Fig. 8B). It differs from the plesiomorphic condition for atherinomorphs where the second pharyngobranchial is never as projected ventrally (Fig. 8A). In the cyprinodontid *Orestias* and the goodeines the whole second pharyngobranchial is reduced, thus not being expanded ventrally. In poeciliines the second pharyngobranchial is also somewhat reduced, without a ventral extension. These cases are considered reversals due to the overall reduction of the bone. Other members of these families (Cyprinodontidae, Goodeidae and Poeciliidae) have the apomorphic condition shared by other cyprinodontoids.

(59) Reduction of the dentition on the second pharyngobranchial. State 0: not reduced; state 1: reduced. The typical second pharyngobranchial of atherinomorphs bears a well-developed tooth plate in which the teeth are irregularly arranged in transverse rows (Fig. 8B). In aplocheiloids, the dentition is very reduced, being represented by a short single row along the posterior border of the bone and often reduced to a single tooth or an absence of teeth in rivulids (Fig. 8A).

#### Neurocranium

(60) Vomerine teeth. State 0: absent; state 1: present. The vomer of aplocheiloids has a weak anteromedial tooth-bearing expansion (Figs. 9B, C). In the majority of aplocheiloids the vomerine teeth are arranged in a small median, rounded patch. In *Aplocheilus* the teeth are arranged along the anterior border of the vomer (Parenti, 1981). In a clade of rivulids (Costa, 1995) all cyprinodontoids, and most remaining atherinomorphs, the vomerine teeth are absent (Figs. 9A, D, E). Parenti (1981) considered the presence of these teeth as ambiguous, being derived for aplocheiloids or lost in cyprinodontoids. Since almost all aplocheilids and basal rivulid clades have vomerine teeth, and cyprinodontoids and other atherinomorphs lack such teeth, the presence of these teeth in aplocheiloids is most parsimoniously interpreted as apomorphic.

(61) Shape of the vomer. State 0: triangular; state 1: Y-shaped. The typical form of the vomer among atherinomorphs is a triangular bone with a posterior median extension (Figs. 9A-C, E). Profundulids have a derived Y-shaped vomer, caused by the narrowing of the lateral portions of the bone (Fig. 9D).



**Figure 9.** Vomer (v), mesethmoid (m) and left lateral ethmoid (e), ventral view, of: **A**, *Melanotaenia* sp.; **B**, *Aphyosemion cameronense*; **C**, *Rivulus brasiliensis*, **D**, *Profundulus candalarius*; and **E**, *Brachyrhaphis terrabensis*. Cartilages not shown.

(62) Mesethmoid. State 0: osseus; state 1: cartilaginous. Aplocheiloids are readily distinguished from most cyprinodontoids and other atherinomorphs by the apomorphic possession of a cartilaginous mesethmoid (Parenti, 1981). An unossified mesethmoid also occurs in most aplocheilichthyine poeciliids (Parenti, 1981; Costa, 1996) and the cyprinodontid genus *Lebias* (Parenti, 1981; Costa, 1997) but phylogenetic hypotheses of interrelationships of both poeciliid and cyprinodontid taxa (Parenti, 1981; Costa, 1996, 1997), support the conclusion that such a character state is not the basal condition for those families.

(63) Distinct process in the anterior portion of the lateral ethmoid. State 0: no process; state 1: a narrow process; state 2: a wide process; state 3: a wide process with a prominent posterior expansion. Parenti (1981) described the presence of a prominent process in the lateral ethmoid for articulation with the autopalatine as a plesiomorphic condition shared by aplocheiloids and profundulids. However, the presence of such a distinct process was not shown to occur in any outgroup to Cyprinodontiformes examined (Fig. 9A). Therefore, the process is herein considered apomorphic. However, there are three distinct shapes of this process, suggesting possible non-homology. These shapes are thus coded as distinct states. Among profundulids there is only a small lateral displacement at the anterior portion of the distinctively narrowed process (Fig. 9D). In aplocheiloids, there is a wide, distinct facet with a process directed posteriorly (Fig. 9B), which is rather prominent in rivulids (Fig. 9C) (Costa, 1990). In non-cyprinodontoid cyprinodontoids, the anterior portion of the lateral ethmoid is similar to the condition in outgroups (Fig. 9E).

(64) Shape of the nasal. State 0: not expanded; state 1: expanded medially. Parenti (1981) hypothesized that the medially expanded nasals in most poeciliids, anablepids, goodeids, and cyprinodontids is a synapomorphy for an assemblage including these families. However, the nasal is expanded in the majority of poeciliids, anablepids and cyprinodontids (Fig. 10A), but never in goodeids (Fig. 10B). In fact, goodeids share another apomorphic condition of the nasal which corresponds to character 65 (nasals in close proximity).

(65) Relative position of nasals. State 0: widely separated; state 1: positioned in close proximity. Uyeno & Miller (1962) noted that the space between the nasals is narrower in *Empetrichthys* and *Crenichthys* (both placed in the Goodeidae by Parenti, 1981), than in *Fundulus* and *Profundulus*. In fact, the nasals of all goodeids are placed more medially than any other taxa analyzed (Fig. 10B), thus constituting an apomorphy for the family.

(66) Shape of neurocranium. State 0: not flattened; state 1: flattened. The neurocranium of aplocheiloids is distinctly flattened, without ventral expansions on the parasphenoid and lateral ethmoid. Other cyprinodontiforms and outgroups have a deeper, dorsally rounded neurocranium, usually with pronounced ventral extensions on the parasphenoid and lateral ethmoid.

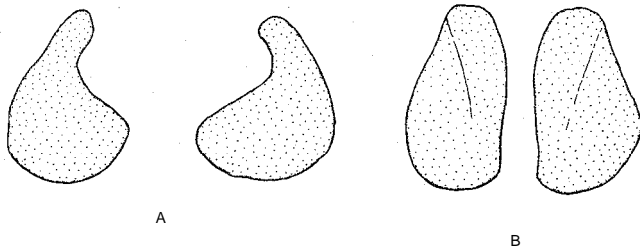
(67) Autopterotic fossa. State 0: not reduced; state 1: reduced. As described by Parenti (1981), the autopterotic fossa of goodeids and most cyprinodontids is apomorphically reduced (Fig. 11B) when compared with the generalized bauplan of cyprinodontiforms, although a unreduced fossa occurs in the cyprinodontid genus *Lebias* (Fig. 11C) and a reduced fossa is found in the fundulid genera *Lucania* and *Leptolucania*. In a

preliminary osteological distinction between *Empetrichthys*, *Crenichthys*, and *Profundulus*, Uyeno & Miller (1962), however, reported larger autopterotic fossa in *Profundulus* than in the other two genera. Parenti (1981) used such an expanded autopterotic fossa as a synapomorphy for profundulids. However, this condition is not distinct in profundulids compared to most cyprinodontiforms.

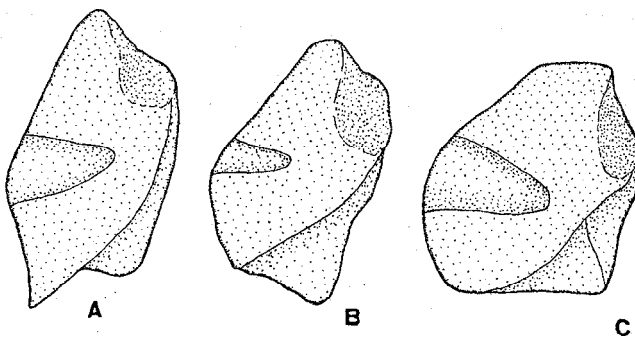
(68) Supraoccipital processes. State 0: crests narrow, short, or slightly elongate; state 1: crests robust and long. As pointed out by Parenti (1981), the supraoccipital processes of ablepids are unique because, in addition to being elongate, they are separated by a notch from the border of the foramen magnum.

(69) Lateral margin of frontal. State 0: not reduced; state 1: reduced. Rivulids are unique among cyprinodontiforms and other atherinomorphs, in having reduced lateral rims to the frontal, resulting in a concave lateral margin of the dorsal surface of the neurocranium (see fig. 2E in Costa, 1995b). In other atherinomorphs the lateral rims are not reduced and the lateral margin of the neurocranium is approximately straight.

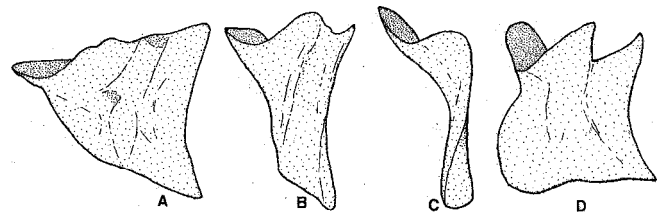
(70) Position of the mesethmoid region. State 0: strongly anterior to the lateral ethmoid; state 1: slightly anterior to the lateral ethmoid. Among non-cyprinodontiform atherinomorphs, the anterior portion of the median portion of the ethmoid region, comprised of the mesethmoid and vomer, is typically placed anterior to the lateral ethmoidal portion (Fig. 9A). In most cyprinodontiforms, the mesethmoid region is only slightly anterior to the lateral ethmoid (Figs. 9B, C, E), constituting an apomorphic condition. However, fundulids, profundulids, and most goodeids, possess an anteriorly displaced mesethmoid region similar to the plesiomorphic state for atherinomorphs (Fig. 9D).



**Figure 10.** Nasals, dorsal view, of **A**, *Cubanichthys cubensis*; and **B**, *Zoogoneticus quitzeensis*.



**Figure 11.** Left autopterotic, ventral view, of **A**, *Profundulus candalarius*; **B**, *Crenichthys baileyi*; and **C**, *Lebias dispar*.



**Figure 12.** Left lacrimal, lateral view, of: **A**, *Atherinella brasiliensis*; **B**, *Aphyosemion cameronsense*; **C**, *Neofundulus paraguayensis*; and **D**, *Lucania goodei*.

#### Infraorbital series

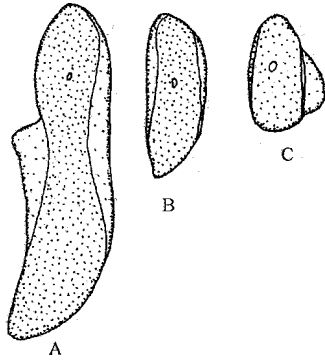
(71) Shape of lacrimal. State 0: approximately triangular; state 1: approximately rectangular. Non-cyprinodontiform atherinomorphs have a wide, triangular lacrimal (Fig. 12A). Most aplocheiloids have a modified triangular lacrimal (see character 72) (Figs. 12B, C). In contrast, cyprinodontoids are unique in having an anteriorly expanded ventral portion of the lacrimal, resulting in a rectangular shape (Fig. 12D).

(72) Reduction and torsion of the lacrimal. State 0: flat, posterior rim wide; state 1: slightly twisted, posterior rim reduced, bone largely limited to the canal; state 2: very twisted and narrow, slender, with canal vestigial. Parenti (1981) recognized a narrow and twisted lacrimal as synapomorphic for aplocheiloids and a lacrimal with obsolescent sensory canal as synapomorphic for rivulids, corresponding to states 1 and 2. However, the apomorphic state shared by aplocheilids is more precisely defined as a reduction of the rim posterior to the sensory canal associated with a slight torsion (Fig. 12B), as opposed to being wide and flat as in other atherinomorphs (Figs. 12A, D). In rivulids the lacrimal is strongly twisted and narrowed (Fig. 12C). In *Aplocheilus* the lacrimal is similar to that observed in outgroups, a hypothesized reversal. A narrow lacrimal associated with a reduction of the sensory canal is also present in some cyprinodontoids (e.g. *Megupsilon* [Costa, 1997]), which lack the characteristic twisted lacrimal of rivulids.

(73) Dermosphenotic. State 0: elongate; state 1: short; state 2: minute. Parenti (1981) considered the reduced dermosphenotic of rivulids (Fig. 13C) as synapomorphic for the family. However, aplocheilids also have a reduced dermosphenotic (Fig. 13B), intermediate between the minute dermosphenotic of rivulids and the elongate dermosphenotic of cyprinodontoids and other atherinomorphs (Fig. 13A). The dermosphenotic of rivulids is further characterized by its approximately flat to slightly concave shape, which contrasts with the deeply concave shape of other groups, and which is associated with the extreme reduction of the sensory canal in rivulids.

#### Pectoral fin and girdle

(74) Position of pectoral-fin insertion. State 0: lateral; state 1: ventrolateral. The apomorphic lowset pectoral girdle of all cyprinodontiforms minus poeciliids described by Parenti (1981, figs. 7 and 8) is confirmed. The condition also present in *Aplocheilus* is considered a homoplasy.



**Figure 13.** Left dermosphenotic, dorsolateral view, of: A, *Cubanichthys cubensis*; B, *Aphyosemion camerounense*; and C, *Neofundulus paraguayensis*.

(75) Shape of the supracleithrum. State 0: narrow to slightly broad ventrally; state 1: extremely broad ventrally. Goodeids and profundulids are unique among cyprinodontiforms and other atherinomorphs in the marked expansion of the ventral portion of the supracleithrum, where it attaches to the cleithrum (Fig. 14A). Some poeciliine taxa also have an expanded supracleithrum, but never as broad as that in goodeids and profundulids. The character is coded as primitive for poeciliids in the data matrix because aplocheilichthyines and basal clades of poeciliines have the plesiomorphic condition.

(76) Fusion of the supracleithrum with the posttemporal. State 0: absent; state 1: present. As discussed by Parenti (1981), aplocheilids are unique among cyprinodontiforms in having the supracleithrum completely fused to the posttemporal, thereby forming a single structure.

(77) First postcleithrum. State 0: present; state 1: absent. The absence of the first postcleithrum was used as synapomorphy for rivulids by Parenti (1981) and Costa (1990a), conclusions in agreement with the present analysis. This bone is also absent in *Orestias*, *Anableps*, and several poeciliids (Parenti, 1981).

(78) Shape of the first postcleithrum. State 0: slender; state 1: scale-like (Parenti, 1981). As discussed by Parenti (1981), cyprinodontiforms are unique among atherinomorphs in having a large, scale-like first postcleithrum, instead of a narrow bone. Since the first postcleithrum is absent in rivulids (Parenti, 1981; Costa, 1990a) the condition is coded as unknown for this family.

(79) A notch on the posterior border of cleithrum. State 0: absent; state 1: present. A second character of the pectoral girdle unique to goodeids and profundulids is the presence of a notch on the posterior border of the cleithrum (Fig. 14A). This notch is absent in other cyprinodontiform taxa (Figs. 14B, C).

(SO) Concavity on the posterior region of the coracoid. State 0: moderate; state 1: deep. Fundulids are unique among cyprinodontiforms in having a pronounced concavity on the posterior portion of coracoid below the fourth radial (Fig. 14B), rather than having the slight concavity in other taxa (Figs. 14A, C).

(81) A distinct expansion on the posteroventral border of the cleithrum. State 0: absent; state 1: present. Only in fundulids is there a posterior expansion of the posteroventral border of the cleithrum (Fig. 14B). In all other cyprinodontiforms the posteroventral border of the cleithrum is never as expanded (Figs. 14A, C).

(82) Posterior extent of the dorsal portion of the cleithrum. State 0: not expanded; state 1: expanded posteriorly. The cleithrum of cypsinodontids has an apomorphic posterior expansion (Fig. 14C) which is absent in other cyprinodontiform taxa (Figs. 14A, B). An exception occurs in the cyprinodontid genus *Orestias*, which has a apomorphically reduced coracoid (Costa, 1997).

#### Pelvic fin and girdle

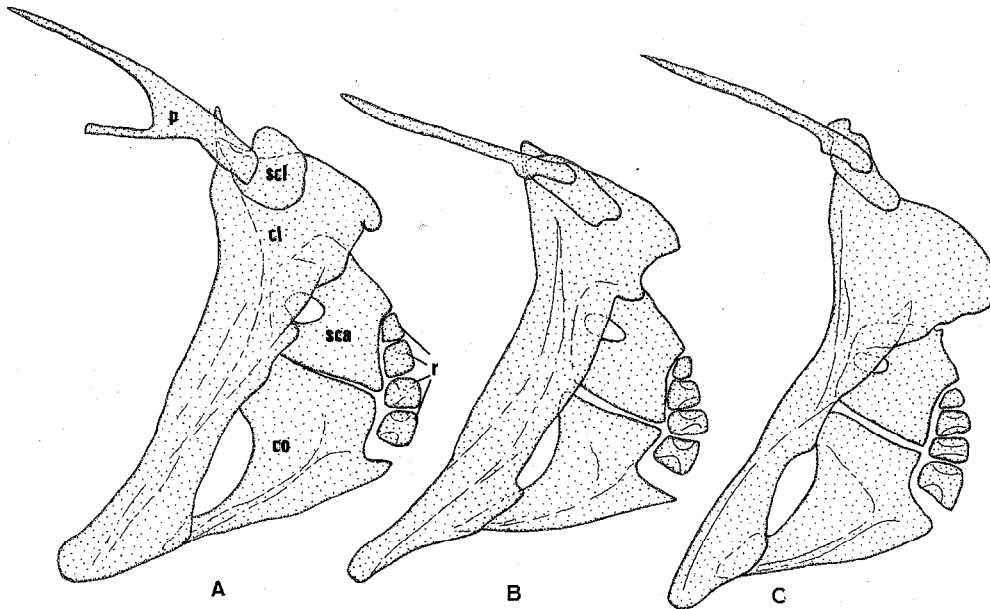
(83) Medial process of the pelvic girdle. State 0: long; state 1: short. As described by Parenti (1981) the pelvic girdle of aplocheiloids has a short medial process (Fig. 15B) in contrast to the long process in other atherinomorphs (Fig. 15A). This apomorphic condition was also observed in some goodeine taxa (e.g. *Zoogoneticus* and *Girardinichthys*).

(84) Anteromedial process of the pelvic girdle. State 0: present; state 1: absent. All examined atherinomorphs other than cyprinodontiforms have a distinct anteromedial process on the pelvic girdle (Fig. 15A), this is considered plesiomorphic for this group. In contrast, no cyprinodontiform has such a process (Fig. 15B).

(85) Placement of pelvic fins, described as the relative position of the pelvic-fin insertion and pleural ribs. State 0: usually between the pleural ribs of vertebrae eight and 11, sometimes between the pleural ribs of vertebrae six and eight; state 1: between the pleural ribs of vertebrae three and six. Parenti (1981) described an anteriorly positioned pelvic girdle as apomorphic for poeciliids. This is, in part, supported in the present study, since the more anteriorly positioned pelvic fin, herein more precisely expressed by the position of the pelvic-fin base relative to pleural ribs, is found not only in all poeciliids examined, but also in all cyprinodontids. Additionally, the pelvic-fin insertion is also positioned anteriorly in a fundulid clade comprising of at least *Lucania* and *Leptolucania*, but not representing the basal condition for the Fundulidae.

#### Caudal fin and skeleton

(86) Symmetry of the caudal fin skeleton. State 0: asymmetrical; state 1: symmetrical. Cyprinodontiforms differ from other acanthomorphs in their symmetrical caudal-fin skeleton as discussed by Rosen (1964) and Parenti (1981). The caudal skeleton consists of a single epural similar to the parahypural in position and shape, and fused hypurals which form together one or two approximately equal plates, lacking distinctive ural centra (Fig. 16). This contrasts with two or three epurals much smaller than the parahypural, and the unfused or asymmetrical plates with distinctive ural centra in other atherinomorphs. Exceptions to this pattern include some species of *Aplocheilichthys* and *Epiplatys* which have a slightly divided dorsal hypural



**Figure 14.** Left pectoral girdle, lateral view, of: **A**, *Profundulus guatemalensis*; **B**, *Fundulus luciae*; and **C**, *Cubanichthys cubensis*. Abbreviations: cl, cleithrum; co, coracoid; p, posttemporal; r, pectoral radials; sca, scapula; and scl, supracleithrum. Postcleithra and cartilages not represented.

plate (Parenti, 1981). The absence of hypochordal musculature in cyprinodontiforms as described by Rosen (1964) has been considered to be associated to the latter condition (Parenti, 1981), an assumption followed in the present study.

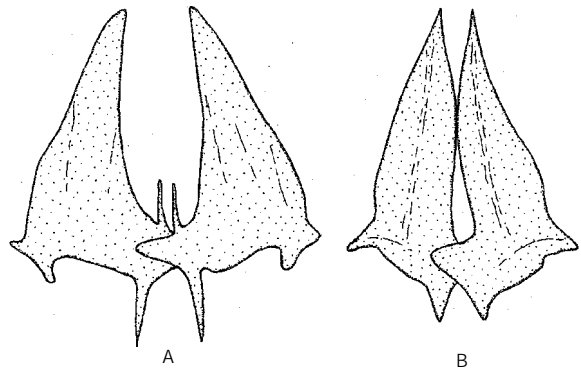
(87) Shape of the caudal fin. State 0: forked; state 1: usually truncate or rounded, never forked. Most atherinomorphs have a forked caudal fin, the hypothesized plesiomorphic condition for the group, which also occurs in basal representatives of all non-cyprinodontiform clades. In contrast, the caudal fin of the cyprinodontiforms are truncate, subtruncate, or rounded, as pointed out by Rosen (1964). In some taxa, dorsal and ventral fin extensions are present, but not a true forked caudal fin. This condition was described by Parenti (1981), but formally employed as synapomorphy in Rosen & Parenti (1981). In addition, the bases of the upper and lower caudal-fin rays of the cyprinodontiforms are not distinctly more robust and longer than the bases of central rays, unlike the condition occurring in taxa with a bilobate caudal fin. This apomorphic condition is associated with the absence of the bilobate shape, and therefore it is not included as a distinct character.

(88) Fusion of the hypural elements. State 0: median horizontal gap between the dorsal and ventral hypurals; state 1: hypurals fused to form a single plate. In non-cyprinodontiform atherinomorphs, the dorsal and ventral hypural elements corresponding to hypurals three, four and five, and hypurals one and two, respectively, are clearly divided by a median horizontal gap. This is also the condition for aplocheiloids (Fig. 16A), since basal taxa of both rivulids and aplocheilids share this generalized bauplan, although a cynolebiatin clade among rivulids and the aplocheilid genus *Nothobranchius* have an entirely fused hypural plate. In cyprinodontoids, almost all included taxa have a completely fused hypural plate (Fig.

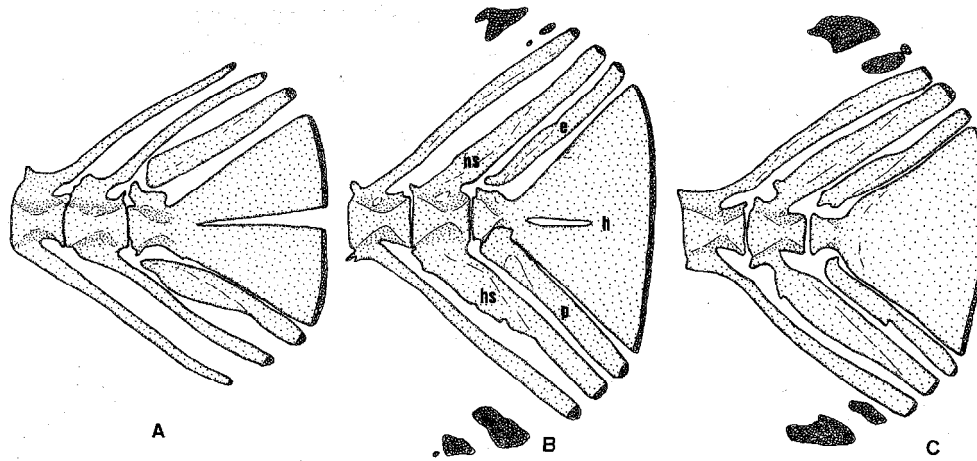
16C). Some poeciliines have a median horizontal fissure, but this is restricted to the anterior portion, not forming a complete gap between the dorsal and ventral elements (Fig. 16B). A reversal of this apomorphic pattern is found in *Anableps* in which there are separate dorsal and ventral plates.

(89) Caudal accessory cartilages. State 0: present; state 1: absent. Aplocheiloids are unique among atherinomorphs in lacking caudal accessory cartilages (Fig. 16A).

(90) Shape of the neural and hemal spines of the preural centrum two. State 0: wide; state 1: narrow. The neural and hemal spines of the preural centrum 2 of rivulids are narrow, not distinctively wider than the spines of other vertebrae (Fig. 16A). In contrast, in all other cyprinodontiform families and outgroups, these spines are much wider than the spines of the vertebrae anterior to preural centrum 2 (Figs. 16B, C). Some members of the aplocheilid genus *Aphyosemion* have narrow spines as described for rivulids.



**Figure 15.** Pelvic girdle, dorsal view, of: **A**, *Atherinella brasiliensis*; and **B**, *Aphyosemion cameronsense*.



**Figure 16.** Caudal skeleton, left lateral view, of: **A**, *Rivulus brasiliensis*; **B**, *Alfaro huberi*; and **C**, *Garmanella pulchra*. Abbreviations: e, epural; h, hypurals; hs, haemal spine; ns, neural spine; and p, parhypural. Dots indicate bone, and circles cartilage.

(91) Shape and position of the proximal end of the parhypural. State 0: robust with paired dorsal processes overlapping the preural centrum; state 1: paired dorsal processes not or barely contacting the preural centrum; state 2: laminar, without dorsal paired process, not contacting the preural centrum. In most cyprinodontiforms and outgroups, the proximal portion of the parhypural is robust, with paired dorsal processes (Fig. 16B). In cyprinodontids, the parhypural and preural centrum are usually not in contact (Fig. 16C), or, in some taxa, the proximal tip of the parhypural barely contacts the preural centrum. In aplocheiloids, this proximal portion is thin, laminar, and lacks a paired dorsal extension (Fig. 16A). An exception occurs in *Aplocheilus* which resembles the plesiomorphic state.

(92) A constriction of the proximal portion of the neural and hemal spines of the preural centrum 2. State 0: absent; state 1: present. Cyprinodontids are unique among cyprinodontiforms in having the proximal portion of the neural and hemal spines of preural centrum 2 constricted, usually bearing a distinct process on the anterior margin (Fig. 16C). Other cyprinodontiforms and outgroups lack this constriction (Fig. 16B).

#### Dorsal and anal fins and fin supports

(93) Shape of the distal radial of the anal fin. State 0: compact, without ventral extensions; state 1: with an expanded posteroventral rim. Aplocheiloids have a distinctly shaped distal radial of the anal fin, resulting from the expanded posteroventral rim (Fig. 17B). This does not occur in cyprinodontoids and the other atherinomorphs examined (Fig. 17A).

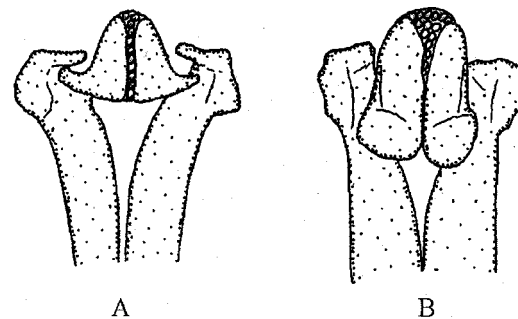
(94) Attachment of the first dorsal-fin rays. State 0: One long first ray attached to two proximal radials; state 1: One long fin ray attached to two proximal radials, preceded by one or two short fin rays. Parenti (1981) cited a well-developed first dorsal-fin ray contacting the two first proximal radials, resulting from the loss of an anterior fin ray, as a synapomorphy of cyprinodontoids. Parenti (1981) recognized this ray as plesiomorphically retained in aplocheiloids. However, in beloniforms as in cyprinodontoids, there is a long fin ray connected

to the first two proximal radials and not preceded by anterior fin rays. In atheriniforms, which have two dorsal fins, the second dorsal fin is homologous to the single dorsal fin of beloniforms and cyprinodontiforms (Parenti, 1993) and the attachment of the first ray and anterior fin support is similar to that of cyprinodontoids. Therefore, the presence of short anterior dorsal-fin rays is parsimoniously interpreted as apomorphic for aplocheiloids.

#### Vertebrae

(95) Position of the first pleural rib. State 0: on the third vertebra; state 1: on the second vertebra. Cyprinodontiforms differ from other atherinomorphs in having the first pleural rib articulated with the parapophysis of the second vertebra rather than the third (Rosen, 1964; Parenti, 1981).

(96) Relative position of neurapophyses on the first vertebra. State 0: united; state 1: separated. Aplocheiloids exhibit the plesiomorphic position and medial union of neurapophyses of the first vertebra (Fig. 18A). In cyprinodontoids, in contrast, the neurapophyses are separate (Fig. 18B), other than for sometimes being in contact via a transverse narrow medial expansion which forms a bridge between the bases of the neurapophyses (Fig. 18C).



**Figure 17.** Base of fifth anal-fin ray and adjacent distal radial, dorsoposterior view, of: **A**, *Lucania goodei*; and **B**, *Neofundulus paraguayensis*. Dots indicate bone, and circles cartilage.

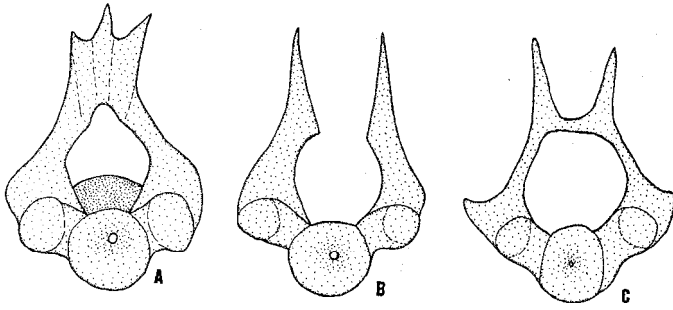


Figure 18. First vertebra, anterior view, of: A, *Neofundulus paraguayensis*; B, *Fundulus majalis*; and C, *Profundulus guatemalensis*.

(97) A median neural spine on the first vertebra. State 0: absent; state 1: present. As described by Costa (1990a), rivulids are unique among cyprinodontiforms in having a distinct, well-developed median neural spine between the neuropophyses (Fig. 18A). Some deep-bodied aplocheilid taxa (*Nothobranchius*) have a median neural spine, but this is not the basal condition for the Aplocheilidae.

#### Lateralis system

(98) Supraorbital lateralis system. State 0: canals closed and well-developed; state 1: canals open with neuromasts exposed externally. Parenti (1981) reported a reduced sensory pore system of the head as synapomorphic for aplocheiloids. In fact, the system is not reduced in aplocheiloids, but the supraorbital portion is modified as open canals with exposed neuromasts. Only in rivulids are all canals open, but some cynolebiatines have the most elaborate neuromast system among cyprinodontiforms, comparable only to that exhibited by the cyprinodontid genus *Orestias* (Parenti, 1981). Open canals also occur in some cyprinodontoid taxa, often among poeciliids (Rosen & Mendelson, 1960; Costa, 1996).

(99) Reduction of canal on the nasal. State 0: not reduced; state 1: reduced. Parenti (1981) described an apomorphic supraorbital canal in poeciliids, consisting of recessed neuromasts on the middle section of the canal. The apomorphic condition exhibited by poeciliids is better defined as a short anterior section of supraorbital canal that lies on the nasal bone, which contrasts with the longer corresponding canal section in most other cyprinodontoids.

#### General morphology of the head

(100) Shape of the anterior naris. State 0: flat, tissue around opening not forming a distinct fleshy structure; state 1: opening situated on a prominent fleshy structure; state 2: opening at the tip of a distinctively cylindrical structure. Parenti (1981) proposed a tubular anterior naris as synapomorphic for aplocheiloids and cited the homoplastic occurrence of similar nares in two cyprinodontoid taxa (*Anableps* and *Cubanichthys*). This agrees, in part, with the results of the present study. Another distinct condition shared by profundulids is a slightly prominent anterior naris instead of the flattened naris

in most other cyprinodontoids. The anterior naris of *Anableps* is somewhat similar to that of aplocheiloids, but the condition of *Cubanichthys* more closely resembles that of profundulids. Both the naris of *Anableps* and *Cubanichthys* are considered independent acquisitions, rather than representing the basal condition for their respective families.

(101) Position of the mouth. State 0: superior; state 1: terminal. Parenti (1981) defined fundulids by having, among other derived features, the snout pointed and elongate anteriorly. According to the present study, the snout of some fundulids is judged somewhat pointed compared with cyprinodontoids. However, most fundulids have snouts similar to those of other cyprinodontoids. Therefore, the condition described by Parenti (1981) is rejected as diagnostic for fundulids. However, most fundulids have a terminal mouth, a condition also present in most anablepids (Ghedotti, this volume), profundulids, and most goodeids, including their basal groups. In addition, a terminal and pointed snout is found in the clade consisting of *Aplocheilus* and *Pachypanchax*.

(102) Attachment of the branchiostegal and opercular membranes. State 0: branchiostegal membrane separate from the opercular membrane; state 1: branchiostegal and opercular membranes united. As discussed by Parenti (1981) and confirmed in a subsequent phylogenetic study (Costa, 1990a), rivulids are unique among cyprinodontiforms in having the branchiostegal and opercular membranes coalesced, rather than folded.

(103) Orbital rim attachment. State 0: free; state 1: attached. As described by Parenti (1981) aplocheiloids have an attached orbital rim. The orbital rim is secondarily free dorsally in a derived clade within the Aplocheilidae (Parenti, 1981), in contrast to the entirely free rim of cyprinodontoids and other atherinomorphs.

#### Scales

(104) Head squamation pattern. State 0: scales arranged transversely, a central scale (A-scale according to Hoedeman's, 1956 terminology) with free posterior border; state 1: scales arranged circularly around a central scale, thus without free borders. The circular squamation pattern was considered synapomorphic for rivulids by Parenti (1981). Since this pattern occurs only in some members of the Rivulidae, Costa (1990a) contested its use as a synapomorphy for the whole family. However, this pattern is herein considered the basal condition for the family.

(105) Number of radii in the anterior abdominal scales. State 0: four to six; state 1: 12 to 16; state 2: 20 to 25. Radii of scales of the cyprinodontiforms are numerous when compared with other atherinomorph taxa, which have between four and six radii. Aplocheiloids have between 20 and 25 and cyprinodontoids between 12 and 16 radii.

#### Color patterns

(106) Sexual dimorphism in color pattern. State 0: males and females with approximately the same color pattern; state 1: males with color pattern much more elaborate than in females.

As discussed by Parenti (1981), aplocheiloids are unique among atherinomorphs in having males with more elaborate color patterns than those of females. In fact, males of aplocheiloid species are often gorgeously pigmented, making these fish very popular in the aquarium trade, and sometimes making it difficult to determine if males and females from a given locality belong to the same species. In contrast, in cyprinodontoids, a slight sexual dimorphism in color patterns may be noted, but the overall pattern is very similar in both sexes. An exception occurs in the South American poeciliid genus *Poecilia*, subgenus *Lebistes*, in which the sides of body and fins of males are very colorful (Rosen & Bailey, 1963; Costa & Sarraf, 1997). This pigmentation is considered homoplastic to that in aplocheiloids.

#### Non-informative characters

**(I)** Dorsal process of the maxillaries with a distinct lateral indentation, attributed to anablepids and poeciliids by Parenti (1981). No distinct indentation in the dorsal process of the maxilla was found that could be considered independent of the shape of the dorsal process (character 2). This process in poeciliids and anablepids is similar to that in cyprinodontids, in being wide (Fig. 1G).

**(II)** Maxilla with a straight proximal arm; attributed to cyprinodontoids minus profundulids and fundulids by Parenti (1981). This condition is indistinguishable among cyprinodontoid taxa.

**(III)** Lateral arm of the maxilla greatly expanded; attributed to cyprinodontids by Parenti (1981). The lateral arm of the maxilla of cyprinodontids does not have apomorphic expansions and does not differ in morphology from the condition in other cyprinodontoids.

**(IV)** Articular (= angulo-articular) greatly reduced; attributed to goodeids by Parenti (1981). The angulo-articular of goodeids is not distinctly reduced (Fig. 3C).

**(V)** Autopalatine projecting anterior to the lateral ethmoid; attributed to fundulids by Parenti (1981). The autopalatine of fundulids barely projects anterior to the lateral ethmoid and is identical to the condition in most other cyprinodontoids.

**(VI)** Interarcual cartilage attaching directly to the lateral surface of the second pharyngobranchial, attributed to aplocheilids by Parenti (1981). This condition does not differ from the basic attachment pattern of the interarcual cartilage in atherinomorphs, including cyprinodontoids.

**(VII)** Interarcual cartilage arising from the base of the first epibranchial and attaching to the second pharyngobranchial; attributed to all cyprinodontiforms by Parenti (1981). Basal atherinomorphs possess an interarcual cartilage which has a tip attached to a well-developed uncinatous process of the first epibranchial, and another tip joined to the lateral portion of the second pharyngobranchial (Rosen & Parenti, 1981). The apomorphic condition described by Parenti (1981) for cyprinodontiforms is derived in the absence of an uncinatous process, with the interarcual cartilage becoming directly attached to the basal cartilage of first epibranchial. However, the loss of the uncinatous process is not unique for cyprinodontiforms, but

instead synapomorphic for a clade comprising of cyprinodontiforms and beloniforms (Rosen & Parenti, 1981). Differences between cyprinodontiforms and beloniforms are due to the latter taxon possessing an apomorphic reduction of the interarcual cartilage, separating it from second pharyngobranchial.

**(VIII)** Reduction of the interarcual cartilage; attributed to cyprinodontoids by Parenti (1981). The basal condition of the interarcual cartilage for cyprinodontoids does not differ from the condition exhibited by other atherinomorphs. In contrast, some aplocheiloid taxa seem to have an apomorphically elongate interarcual cartilage, but the distribution of that character among aplocheiloids indicates that it did not arise at the base of that clade.

**(IX)** Toothplate of the fourth pharyngobranchial greatly reduced; attributed to cyprinodontids by Parenti (1981). According to the present analysis and the phylogenetic study of cyprinodontids (Costa, 1997), a reduced fourth pharyngobranchial toothplate occurs in a single cyprinodontid taxa (*Garmanella*) and, thus, does not serve to define the family.

**(X)** Posterior extension of the vomer dorsal to the parasphenoid; attributed to the Aplocheiloidei by Parenti (1981). No aplocheiloid has any portion of the vomer situated dorsal to the parasphenoid. As in other atherinomorphs examined, all aplocheiloids have the vomer located completely ventral to the anterior arm of the parasphenoid. Some rivulids, however, have the ventral rims of parasphenoid ventrally overlapping the posterior portion of vomer, which causes problems in the interpretation of the character.

**(XI)** Lateral ethmoid expanded medially; attributed by Parenti (1981) to rivulids. A slight expansion of the mesial portion of the lateral ethmoid toward the parasphenoid, as in some rivulids (but not all, Fig. 9C), occurs in most cyprinodontiforms, and does not define that family or any familial assemblage.

**(XII)** Lateral ethmoid expanded medially and oriented so that it lies perpendicular to the frontal; attributed to goodeids and cyprinodontids by Parenti (1981). The lateral ethmoid is variable among cyprinodontoids, but no change in orientation relative to the frontal was observed. This does not represent an apomorphic condition for these taxa.

**(XIII)** Parasphenoid with expanded anterior arm; attributed to poeciliids and anablepids by Parenti (1981). The expansion of the anterior portion of the parasphenoid of poeciliids and anablepids is comparable to that in several other cyprinodontiform taxa, and does not define a clade comprising those families.

**(XIV)** First two to seven middle anal-fin radials fused to the proximal radials; attributed to goodeids by Parenti (1981). This condition was not confirmed in *Crenichthys* and *Empetrichthys*, thus this is parsimoniously interpreted as synapomorphic for goodeines.

**(XV)** Pleural ribs on the first several hemal arches of caudal vertebrae; attributed to poeciliids by Parenti (1981). This condition was not verified in the poeciliid taxa examined. Based on the present data this character does not support the monophyly of the Poeciliidae.

**(XVI)** Inclinator of the anal fin greatly enlarged; attributed to goodeids and cyprinodontids by Parenti (1981). Enlarged inclinator of the anal fin were observed in goodeines as described by Nelson (1975). However, the inclinator of cyprinodontids and oviparous goodeids are not distinctively enlarged relative to those of other cyprinodontoids, except for poeciliines, which have elaborate anal-fin musculature in males associated with internal fertilization, as described by Rosen & Gordon (1953). In fact, in *Fundulus* the inclinator is longer than in cyprinodontids. Thus, this condition is rejected as a synapomorphy of goodeids plus cyprinodontids.

**(XVII)** Pouch created by scales surrounding the urogenital opening of females; attributed to poeciliids and anablepids by Parenti (1981). Females of cyprinodontiforms have a pouch-like urogenital opening formed by flaps of expanded tissue anterior to the anal-fin origin. Scales may or may not cover the borders of those flaps. The edges of the flaps are usually naked or coincident with scale borders, but when scales extend beyond them, a pouch of scales surrounding the urogenital opening is formed. A moderate pouch occurs in some poeciliines (e.g. *Alfaro*), but a unique, distinctive pouch occurs in both males and females of African aplocheilichthyines, as described by Clausen (1967), as well as in *Fluviphylax*, although it is not as pronounced in this latter genus. A pouch absent is in *Jenynsia* and *Anableps*. Since many poeciliids do not possess a true scale pouch, it cannot be synapomorphic for this family but only for the subfamily Aplocheilichthyinae.

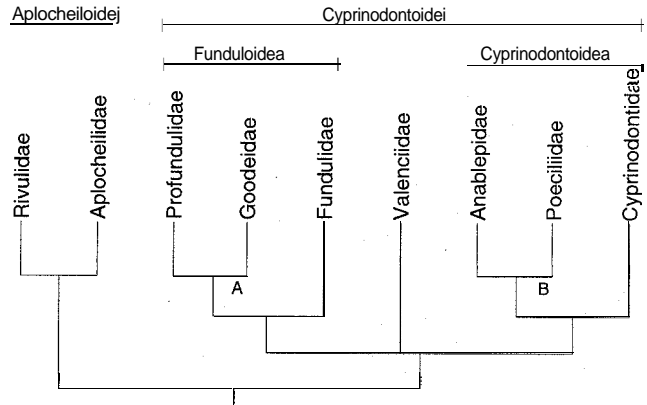
**(XVIII)** Long developmental period comprising 12 or more days; attributed to Cyprinodontiformes by Parenti (1981). This derived condition was subsequently considered a synapomorphy for atherinomorphs by Parenti (1993).

### Classification

The three most parsimonious phylogenetic hypotheses supported by the 106 characters listed and discussed above are summarized in the consensus tree in Fig. 19, which is the basis for the classification below. Character numbers are equivalent to those presented in the character analysis above. The symbol “\*” indicates homoplastic features and “-” reversals.

#### Order Cyprinodontiformes Berg

Diagnosis: A distinct anterior expansion on the alveolar arm of premaxilla (13. 1), tendon of the superficial (A,) division of *adductor mandibulae* attached to lacrimal (26. 1), dorsal edge of mesopterygoid reduced (32. 1), urohyal deep (37. 1), ventral process of the lateral portion of second epibranchial absent (55.1) mesethmoid region slightly anterior to lateral ethmoid (70. 1), pectoral-fin insertion positioned ventrolaterally (74. 1), first postcleithrum scale-like (78. 1), anteromedial process of pelvic girdle absent (84.1), caudal fin skeleton symmetrical (86.1), caudal fin truncate or rounded (87.1), first pleural rib on second vertebra (95. 1), and 12-16 radii on anterior abdominal scales (105.1).



**Figure 19.** Strict consensus cladogram of the three equally most parsimonious phylogenetic hypotheses and classification of the Cyprinodontiformes (length: 129; consistency index: 0.90; retention index: 0.86; rescaled consistency index: 0.77). Characters, character states, and synapomorphies for nodes are listed and discussed in the text.

#### Suborder Aplocheiloidei Bleeker

Diagnosis. Dorsal process of maxilla short, anteriorly directed, not parallel to ventral process (1.1); main axis of the ventral process of maxilla slightly curved, tip directed posteriorly (4. 1), coronoid process of anguloarticular reduced (23. 1), lateral flange of hyomandibula expanded posterodorsally (35.1), anterior portion of basihyal widened (43.1), a distinct anteromedial process on second hypobranchial directed toward second basibranchial (46.1), anterior cartilage head of fifth ceratobranchial narrow and reduced (49.1), membranous aperture between fourth and fifth ceratobranchials reduced (52.1), a distinct posterior process on fourth epibranchial (57. 1), dentition on second pharyngobranchial reduced (59.1), vomerine teeth present (60.1) mesethmoid cartilaginous (62.1), a wide process on the anterior portion of lateral ethmoid (63.2), neurocranium flattened (66.1), lacrimal slightly twisted with posterior rim reduced and bone formed mainly by canal (72.1), dermosphenotic short (73.1), medial process of pelvic girdle short (83.1), caudal accessory cartilages absent (89.1), distal radial of anal fin with an expanded posteroventral rim (93.1), proximal end of the parhypural laminar, without dorsal paired process, and not contacting preural centrum (91.2), anterior portion of dorsal fin with one long ray attached to two proximal radials and preceded by one or two short rays (94.1), supraorbital canals open with neuro-masts exposed externally (98.1), anterior naris opening at the tip of a distinctively cylindrical structure (100.2), orbital rim attached (103.1), 20 to 25 radii on anterior abdominal scales (105.2), and males with color pattern much more elaborate than in females (106.1).

#### Family Rivulidae Myers

Diagnosis. Ventral process of maxilla bent and directed posteriorly, median portion expanded anteriorly, producing a triangular shape (4.2), ventral portion of autopalatine short, not contacting quadrate (28.1) preopercle thin, C-shaped,

with a reduced median rim and vestigial sensory canal (36.1), basihyal cartilage reduced, restricted to anterior part of basihyal (44.1\*), a wide process with a prominent posterior expansion on the anterior portion of lateral ethmoid (63.3), lateral margin of frontal reduced (69.1), lacrimal very twisted and narrow and slender, with canal vestigial (72.2), dermosphenotic minute (73.2), first postcleithrum absent (77.1), neural and hemal spines of the preural centrum two narrow (90.1) a median neural spine on the first vertebra (97.1), branchiostegal and opercular membranes united (102.1), and frontal scales arranged circularly around a central A-scale (104.1).

#### Family Aplocheilidae Bleeker

Diagnosis. Posterior tip of the ascending process of premaxilla curved medially (15.1), ventral process of anguloarticular expanded (22.1), and supracleithrum and posttemporal coossified (76.1).

#### Suborder Cyprinodontoidei Gill

Diagnosis. Ethmomaxillary ligament absent (8.1), rostral cartilage small or absent, ligaments absent, rostral cartilage, when present, embedded in thickened and elongate connective tissue between ventral processes of maxilla (9.1), meniscus between ventral process of maxilla and ascending process of premaxilla absent (10.1), posterior indentation on the alveolar arm of premaxilla (14.1), dentary deep (19.1), head of autopalatine bent anteriorly, displaced laterally relative to the main axis of the bone (27.1), metapterygoid absent (34.1) dorsal hypohyal absent (4.1), basihyal cartilage reduced, restricted to anterior part of basihyal (44.1\*), first basibranchial absent (45.1) ventral process of fourth ceratobranchial expanded medially (48.1), ventral process of the lateral portion of second epibranchial absent (55.1), second pharyngobranchial expanded ventrally (58.1), lacrimal approximately rectangular (71.1), hypural elements fused to form a single plate (88.1) and neuropophyses on the first vertebra separated (96.1).

#### Superfamily Funduloidea, new usage

Diagnosis. Dorsal process of maxilla vestigial (1.2) ventral process of maxilla abruptly curved ventrally (7.1), mesethmoid region distinctly anterior to lateral ethmoid (70.1-), and mouth terminal (10.1.1\*).

#### Family Fundulidae Jordan & Gilbert

Diagnosis. Main axis of the ventral process of maxilla long, directed anteriorly (5.1), a small cartilage posterior to rostral cartilage (12.1), premaxilla elongate (17.1), a prominent dorsomedial flange of autopalatine, sometimes forming a short process (29.1\*), dorsal process of urohyal vestigial or absent (38.1) a distinct anteriorly expanded rim on anterior border of the first hypobranchial (47.1), teeth on posterior half of third ceratobranchial (50.1), concavity present on the posterior region of the coracoid (80.1), and a distinct expansion on the posteroventral border of the cleithrum (8.1.1).

#### Unnamed clade A (Goodeidae plus Profundulidae)

Diagnosis. Rostral cartilage transversely elongated (11.1), concavity present on the posterior margin of quadrate (33.1), a ventral process on the lateral portion of second epibranchial (55.1-), supracleithrum extremely widened ventrally (75.1), and a notch on the posterior border of cleithrum (79.1).

#### Family Goodeidae Jordan

Diagnosis. Cartilaginous head of autopalatine reduced (30.1), ventral portion of first epibranchial very wide, usually forming two separate cartilage heads (54.1), nasals positioned in close proximity (65.1), and autopterotic fossa reduced (67.1").

#### Family Profundulidae Hoedeman & Bronner

Diagnosis. Rostral cartilage and ligaments well-developed (9.1-), 13 to 23 gill rakers on the anterior arm of the first arch (53.1\*), vomer Y-shaped (61.1), a narrow process on the anterior portion of lateral ethmoid (63.1), and anterior naris opening situated in a prominent fleshy structure (100.1).

#### Superfamily Valencioidea, new usage

Diagnosis. As for the family Valenciidae below.

#### Family Valenciidae Parenti

Diagnosis. Rostral cartilage minute or absent, ligaments absent, thin connective tissue between ventral processes (9.2\*), a prominent dorsomedial flange of autopalatine, sometimes forming a short process (29.1\*), ventrolateral flange of urohyal expanded ventrally (40.1), and a cartilage between medial margins of fifth ceratobranchials (5.1.1).

#### Superfamily Cyprinodontoidea Gill

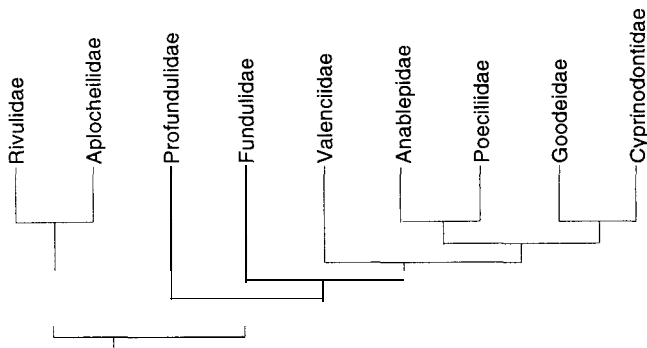
Diagnosis. Dorsal process of maxilla broad (2.1), rostral cartilage minute or absent, ligaments absent, thin connective tissue between ventral processes (9.2\*), premaxillary ascending process shortened (16.1), dorsomedial flange of autopalatine forming a distinctive elongate process (29.2), dorsal process of urohyal bent posteriorly (39.1), and nasal expanded medially (64.1).

#### Family Cyprinodontidae Gill

Diagnosis. A distinct groove on the dorsal process of maxilla (3.1), autopterotic fossa reduced (67.1\*), dorsal portion of the cleithrum expanded posteriorly (82.1), pelvic-fin insertion between the pleural ribs of vertebrae three to six (85.1\*), proximal end of the parhypural with paired dorsal processes not, or barely, contacting preural centrum (91.1), and proximal portion of the neural and hemal spines of the preural centrum 2 constricted (92.1).

#### Unnamed clade B (Anablepidae plus Poeciliidae)

Diagnosis. Distal arm of maxilla distinctively widened (6.1), premaxillary ascending process widened (18.1), posteroventral process of dentary reduced (20.1), and retroarticular and ventral process of anguloarticular long (21.1).



**Figure 20.** Cladogram depicting phylogenetic relationships of Cyprinodontiformes, according to Parenti (1981).

Family Anablepidae Garman

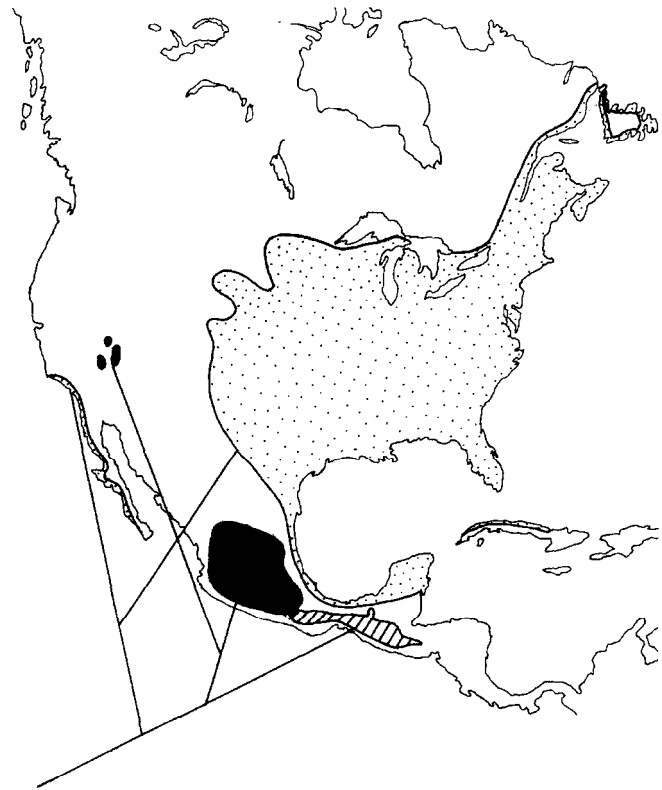
Diagnosis. Teeth tricuspid (2.5.1), 13-23 gill rakers on the anterior arm of the first arch (53.1\*), supraoccipital crests robust and long (68.1) a complete median horizontal gap between dorsal and ventral hypurals (88.1-), and mouth terminal (101.1\*).

Family Poeciliidae Garman

Diagnosis. A pronounced indentation on the anterior base of the coronoid process of anguloarticular (24.1), cartilaginous head of autopalatine wide (3 1. 1), a single terminal condyle on the anterior portion of anterior ceratohyal (42.1) pectoral-fin insertion positioned laterally (74.1-), pelvic-fin insertion between the pleural ribs of vertebrae three to six (85.1\*), and canal on nasal reduced (99.1).

**Discussion**

The monophyly of the order Cyprinodontiformes is herein supported by five apomorphic character states (32.1, 37.1, 70.1, 84.1, and 105.1) not recorded in previous studies. Similarly, the monophyly of the suborders Aplocheiloidei and Cyprinodontoidei is corroborated by 19 (1.1, 4.1, 23.1, 35.1, 46.1,49.1,52.1,57.1,59.1, 60.1,63.2, 66.1,73.1, 89.1,91.2, 93.1, 94.1, 105.2, and 106.1) and seven (44.1, 48.1, 55.1, 58.1, 7 1.1, 88.1, and 96.1) new apomorphic character states, respectively. The monophyly of the all nine included families is supported in the present analysis, which comprises 25 new diagnostic characters at the family level [28.1, 44.1, and 90.1, for the Rivulidae; 22.1 for the Aplocheilidae; 12.1, 17.1, 38.1, 47.1, 50.1, 80.1, and 81.1 for the Fundulidae; 54.1 and 65.1 for the Goodeidae; 61 .1, 63.1, and 100.1 for the Profundulidae; 40.1 and 51.1 for the Valenciidae; 82.1, 91.1 and 92.1 for the Cyprinodontidae; 53.1 and 101.1 for the Anablepidae; and, 24.1 and 3 1.1 for the Poeciliidae]. Monophyly of Cyprinodontiformes and its included suborders and families, as defined by Parenti (1981) and the present study, is also supported in recent studies based on molecular phylogeny (Meyer & Lydeard, 1993; Parker, 1996). On the other hand, Murphy & Collier (1997) also using molecular methodology, obtained



**Figure 21.** Distribution pattern and interrelationships of the clade comprising the families Fundulidae (dotted), Goodeidae (blackened), and Profundulidae (cross-hatched).

evidence contrary to the hypothesis of the Aplocheilidae monophyly. According to these authors, African aplocheilids are closer related to rivulids than to Asiatic (*Aplocheilus*) and Madagascan (*Pachypanchax*) aplocheilids. Although *Aplocheilus* exhibits some conditions apparently plesiomorphic for the Cyprinodontiformes (see discussion on characters 72, 74, 86, and 91 in the character analysis), the monophyly of the Aplocheilidae is unambiguously supported by morphological characters.

The phylogenetic hypothesis advanced herein differs from Parenti's (1981) hypothesis in that the Profundulidae is the sister group of the Goodeidae, as opposed to the Profundulidae constituting the sister group of all other cyprinodontoids, and in having the Goodeidae forming the sister group of the Cyprinodontidae (Figs. 19 and 20). Parenti (1981) defined a clade comprising all cyprinodontoids minus profundulids by four synapomorphies, of which, two are herein considered to be equivocal (characters 16 and 63), and the other two are considered redundant, consisting of a single character state, which is most parsimoniously interpreted as a reversal (character 9). From the three synapomorphies described by Parenti (1981) for the clade comprising goodeids and cyprinodontids, two are herein considered equivocal (characters XII and XVI) and the third is most parsimoniously interpreted as homoplastic (character 67). The three synapomorphies established by Parenti (1981) for the clade comprising

goodeids, cyprinodontids, anablepids, and poeciliids (characters 2, 16, 65) are found to be present in the last three groups, but were found to be absent in goodeids.

On the other hand, the present analysis identifies four synapomorphies for the clade including goodeids, profundulids, and fundulids (the Funduloidea), and five synapomorphies for the clade including goodeids and profundulids, as diagnosed above. Both the monophyly of the Funduloidea and the interrelationships of its included families are supported in a molecular phylogenetic analysis (Meyer & Lydeard, 1993). Furthermore, the sister group relationships between goodeids and profundulids, and between this assemblage and fundulids, indicate an interesting biogeographic pattern, since these taxa exhibit a continuous and approximately disjunct distribution area (Fig. 21). In addition, profundulids and goodeids, are usually found in mountain streams and lakes, at altitudes between 900 and 2100 m (Miller, 1955; Miller & Fitzsimons, 1971). This could be considered a further apomorphic condition for this assemblage, since non-cyprinodontiform atherinomorphs typically inhabit coastal environments, and freshwater atherinomorphs, with a few exceptions (e.g. *Orestias*), do not inhabit mountain streams.

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#### Literature cited

- Aarn & W. Ivantsoff. 1997. Descriptive anatomy of *Cairnsichthys rhombosomoides* and *Iriatherina werneri* (Teleostei: Atheriniformes), and a phylogenetic analysis of Melanotaeniidae. *Ichthyol. Explor. Freshwaters*, 8: 107-150.
- Alexander, R. McN. 1967. Mechanisms of the jaws of some atheriniform fish. *J. Zool.*, London, 151: 233-255.
- Chernoff, B. 1986. Phylogenetic relationships and reclassification of menidiine silverside fishes with emphasis on the tribe Membradini. *Proc. Acad. Nat. Sci. Philadelphia*, 138: 189-249.
- Clausen, H. S. 1967. *Tropical Old World cyprinodonts*. Akademisk Forlag, Copenhagen.
- Costa, W. J. E. M. 1990a. Análise filogenética da família Rivulidae (Cyprinodontiformes, Aplocheiloidei). *Rev. Brasil. Biol.*, 50: 65-82.
- Costa, W. J. E. M. 1990b. Description d'une nouvelle espèce du genre *Rivulus* (Cyprinodontiformes, Rivulidae) de l'Amazone orientale. *Rev. Fr. Aquariol.*, 17: 41-44.
- Costa, W. J. E. M. 1991. Description d'une nouvelle espèce du genre *Pamphorichthys* (Cyprinodontiformes: Poeciliidae) du bassin de l'Araguaia, Brésil. *Rev. Fr. Aquariol.*, 18: 39-42.
- Costa, W. J. E. M. 1995a. Two new genera and two new species of the neotropical annual fishes Plesiolebiatini (Cyprinodontiformes: Rivulidae), with studies on the relationships of the tribe. *Rev. Fr. Aquariol.*, 21: 65-74.
- Costa, W. J. E. M. 1995b. Revision of the neotropical annual fish genus *Campellobias* (Cyprinodontiformes: Rivulidae), with notes on phylogeny and biogeography of the Cynopoecilina. *Cybiurn*, 19: 349-369.
- Costa, W. J. E. M. 1996. Relationships, monophyly and three new species of the neotropical miniature poeciliid genus *Fluviphylax* (Cyprinodontiformes: Cyprinodontoidei). *Ichthyol. Explor. Freshwaters*, 7, 11 1-130.
- Costa, W. J. E. M. 1997. Phylogeny and classification of the Cyprinodontidae revisited (Teleostei: Cyprinodontiformes): Are Andean and Anatolian killifishes sister taxa? *J. Comp. Biol.*, 2: 1-17.
- Costa, W. J. E. M. & A. Sarraf. 1997. *Poecilia (Lebistes) minima*, a new miniature poeciliid fish from the Brazilian Amazon. *Ichthyol. Explor. Freshwaters*, 8: 185-191.
- Dyer, B. S. & B. Chernoff. 1996. Phylogenetic relationships among the atheriniform fishes (Teleostei, Atherinomorpha). *Zool. J. Linn. Soc.*, 117: 1-69.
- Farris, J. S. 1988. "Hennig86, Version 1.5" program and documentation, Farris, Port Jefferson Station, New York.
- Garman, S. 1895. The cyprinodonts. *Mem. Mus. Comp. Zool.*, 19: 1-179.
- Ghedotti, M. J. This volume. Phylogeny and classification of the Anablepidae (Teleostei: Cyprinodontiformes).
- Gosline, W. A. 1949. The sensory canals of the head in some cyprinodont fishes, with particular reference to the genus *Fundulus*. *Oct. Pap. Mus. Zool. Univ. Michigan*, 519: 1-17.
- Grant, E. C. & B. R. Riddle. 1995. Are the endangered springfish (*Crenichthys* Hubbs) and poolfish (*Empetrichthys* Gilbert) fundulines or goodeines? A mitochondrial DNA assessment. *Copeia*, 1995: 209-212.
- Helfman, G. S., B. B. Collette & D. E. Facey. 1997. *The diversity of fishes*. Blackwell Science, Malden, 528 p.
- Hoedeman, J. J. 1956. Die bisher beschriebenen Formen und Arten der Gattung *Rivulus* Poey. *Aquar. Terrar.*, 1956: 199-202.
- Hubbs, C. L. 1924. Studies of the fishes of the order Cyprinodontes. *Misc. Publ. Mus. Zool. Univ. Michigan*, 13: 1-31.
- Ivantsoff, W., B. Said & A. Williams. 1987. Systematic position of the family Dentatherinidae in relationship to Phallostethidae and Atherinidae. *Copeia*, 1987: 649-658.
- Maddison, W. P., M. J. Donoghue & D. R. Maddison. 1984. Outgroup analysis and parsimony. *Syst. Zool.*, 33: 26-38.
- Meyer, A. & C. Lydeard. 1993. The evolution of copulatory organs, internal fertilization, placentae and viviparity in killifishes (Cyprinodontiformes) inferred from a DNA phylogeny of the tyrosine kinase gene X-src. *Proc. R. Soc. Lond.*, 254: 153-162.
- Miller, R. R. 1955. A systematic review of the Middle American fishes of the genus *Profundulus*. *Misc. Publ. Mus. Zool., Univ. Michigan*, 92: 1-64.
- Miller, R. R. & J. M. Fitzsimons. 1971. *Ameca splendens*, a new genus and species of goodeid fish from Western Mexico, with remarks on the classification of the Goodeidae. *Copeia*, 1971: 1-13.
- Moyle, P. B. & J. J. Cech, Jr. 1996. *Fishes: an introduction to Ich-*

## Appendix A

- thyology. Third edition. Prentice-Hall, Upper Saddle River, 590p.
- Murphy, W. J. & G. E. Collier. 1997. A molecular phylogeny for aplocheiloid fishes (Atherinomorpha, Cyprinodontiformes): The role of vicariance and the origins of annualism. *Mol. Biol. Evol.*, 14: 790-799.
- Myers, G. S. 1931. The primary groups of oviparous cyprinodont fishes. *Stanford Univ. Publ., Bol. Sci.*, 6: 1-14.
- Nelson, J. S. 1994. *Fishes of the World*. 3rd. ed. John Wiley & Sons. New York, 600 p.
- Nelson, G. G. 1975. Anatomy of male urogenital organs of *Goodea atripinnis* and *Characodon lateralis* (Atheriniformes: Cyprinodontidae) and *C. atripinnis* courtship. *Copeia*, 1975: 475-482.
- Parenti, L. R. 1981. A phylogenetic and biogeographic analysis of cyprinodontiform fishes (Teleostei, Atherinomorpha). *Bull. Amer. Mus. Nat. Hist.*, 168: 335-557.
- Parenti, L. R. 1984. A taxonomic revision of the Andean killifish genus *Orestias* (Cyprinodontiformes, Cyprinodontidae). *Bull. Amer. Mus. Nat. Hist.*, 178: 107-214.
- Parenti, L. R. 1993. Relationships of atherinomorph fishes (Teleostei). *Bull. Mar. Sci.*, 170-196.
- Parker, A. 1997. Combining molecular and morphological data in fish systematics: Examples from the Cyprinodontiformes. Pp. 163-188 in: T. D. Kocher & C. A. Stepien (eds.), *Molecular systematics of fishes*, Academic Press, San Diego.
- Rosen, D. E. 1964. The relationships and taxonomic position of the halfbeaks, killifishes, silversides, and their relatives. *Bull. Amer. Mus. Nat. Hist.*, 127: 217-268.
- Rosen, D. E. & R., M. Bailey. 1963. The poeciliid fishes (Cyprinodontiformes), their structure, zoogeography, and systematics. *Bull. Amer. Mus. Nat. Hist.*, 126: 1-176.
- Rosen, D. E. & M. Gordon. 1953. Functional anatomy and evolution of male genitalia in poeciliid fishes. *Zoologica*, 36: 1-47.
- Rosen, D. E. & J. R. Mendelsohn. 1960. The sensory canals of the head in poeciliid fishes (Cyprinodontiformes), with reference to dentitional types. *Copeia*, 1960: 203-210.
- Rosen, D. E. & L. R. Parenti. 1981. Relationships of *Oryzias*, and the groups of atherinomorph fishes. *Am. Mus. Novitates*, 2719: 1-25.
- Stiassny, M. L. J. 1990. Notes on the anatomy and relationships of the bedotiid fishes of Madagascar, with a taxonomic revision of the genus *Rheocles* (Atherinomorpha: Bedotiidae). *Amer. Mus. Novitates*, 2979: 1-33.
- Taylor, W. R. & G. C. Van Dyke. 1985. Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study. *Cybio*, 9: 107-109.
- Uyeno, T. & R. R. Miller. 1962. Relationships of *Empetrichthys erdisi*, a Pliocene cyprinodontid fish from California with remarks on the Fundulinae and Cyprinodontinae. *Copeia*, 1962: 520-532.
- Vari, R. P. 1989. A phylogenetic study of the neotropical characiform family Curimatidae (Pisces: Ostariophysi). *Smithsonian Contr. Zool.*, 471: 1-71.
- Weitzman, S. H. 1962. The osteology of *Blycon meeki*, a generalized characid fish, with an osteological definition of the family. *Stanford Ichthyol. Bull.*, 8: 1-77.
- White, B. N. 1985. Evolutionary relationships of the Atherinopsinae (Pisces: Atherinidae). *Contrib. Sci.*, 368: 1-20.
- Winterbottom, R. 1974. A descriptive synonymy of the striated muscles of the Teleostei. *Proc. Acad. Nat. Sci. Philadelphia*, 125: 225-317.

The following list of material refers to specimens of cyprinodontiform taxa and outgroups examined for the present study. Number of specimens in each lot follows catalogue numbers, with specimens cleared and stained for bone and cartilage (c&s). Order is alphabetical. Most material is deposited in the Universidade Federal do Rio de Janeiro (UFRJ); other institutional acronyms are: AMNH, American Museum of Natural History, New York, CAS, California Academy of Sciences, San Francisco; INPA, Instituto Nacional de Pesquisas da Amazônia, Manaus; MCP, Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre; MNRJ, Museu Nacional, Rio de Janeiro; Rio de Janeiro; MUSM, Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima; MZUSP, Museo de Zoologia, Universidade de São Paulo, São Paulo; UMMZ, Museum of Zoology, The University of Michigan, Ann Arbor; and USNM, National Museum of Natural History, Smithsonian Institution, Washington.

**Cyprinodontiformes - Anablepidae:** *Anableps anableps*: UFRJ 089,2; UFRJ 3419, 1 (c&s); *A. dovii*: UFRJ 3289, 2; UFRJ 3290,2 (c&s); *A. microlepis*: UFRJ 3943, 2; UFRJ 3420, 2 (c&s); *Jenynsia multidentata*: UFRJ 2142, 6; UFRJ 3421, 2 (c&s); *J. unitaenia*: UFRJ 193, 2; UFRJ **3422, 2 (c&s)**. **Aplocheilidae:** *Aphyosemion aureum*: UFRJ 3878, 6; *A. australe*: MZUSP 38469,1 (c&s); *A. cameronense*: UFRJ 621, 2; UFRJ 1154, 1 (c&s); *A. grignardi*: UFRJ 3883, 8; UFRJ 4110,4 (c&s); *A. gulare*: UFRJ 623, 2; UFRJ 626, 1 (c&s); *A. herzogi*: UFRJ 3880,3; *A. splendidum*: UFRJ 3877, 1 (c&s); *A. striatum*: MZUSP 38470,1 (c&s); *Aplocheilus blockii*: UFRJ 3148, 2; UFRJ 3149, 2 (all c&s); *A. dayi*: UFRJ 3142, 2; UFRJ 3143, 2 (c&s); *A. lineatus*: UFRJ 3146, 2; UFRJ 3147, 2 (c&s); *A. panchax*: UFRJ 3140,2; UFRJ 3141, 2 (c&s); *A. weneri*: UFRJ 3144, 2; UFRJ 3145, 2 (c&s); *Epiplatys bifasciatus*: UFRJ 3881,4; UFRJ 4111, 3 (c&s); *E. chaperi*: UFRJ 627, 1; UFRJ 619, 2 (c&s); *E. dageti*: UFRJ 3885, 3; MZUSP 38426, 1 (c&s); *E. fasciolatus*: UFRJ 1151, 1 (c&s); *E. mesogramma*: UFRJ 3874, 2 (c&s); *E. neumanni*: UFRJ 3876, 3; *E. sangmelinensis*: UFRJ 622, 1; UFRJ 1152, 1 (c&s); *Nothobranchius rachovii*: MZUSP 38507, 1 (c&s); MZUSP 38442, 1 (c&s); *Pachypanchax playfairi*: AMNH 20701,4 (c&s); *Roloffia petersi*: UFRJ 624, 1; UFRJ 3685, 2 (c&s). **Cyprinodontidae:** *Cualac tessellatus*: GAS 168742, 1 (c&s); *Cubanichthys cubensis*: USNM 124380, 6; USNM 331917, 4 (2 c&s); *Cyprinodon elegans*: UFRJ 3898, 4; UFRJ 3900, 2 (c&s); *C. macrolepis*: UFRJ 3899, 8; UFRJ 3901, 2 (c&s); *C. variegatus artifions*: UFRJ 3902, 8; UFRJ 3903, 1 (c&s); *C. variegatus variegatus*: UFRJ 3316, 10; UFRJ 3317, 2 (c&s); *Floridichthys carpio*: UFRJ 3449, 11; UFRJ 3425, 4 (c&s); *Garmanella pulchra*: UFRJ 3450, 21; UFRJ 3426, 4 (c&s); *Jordanella jloridae*: UFRJ 3315, 1; UFRJ 3904, 1 (c&s); *Lebias anatoliae splendens*: CAS 168742, 4 (c&s); *L. dispar*: UFRJ 3301, 2; UFRJ 3302, 2 (c&s); *L. fasciatus*: UFRJ 4018, 4; UFRJ 4019, 3 (c&s); *Megupsilon aporus*: UFRJ 3447, 21; UFRJ 3427, 4 (c&s); *Orestias agassii*: UFRJ 3047, 5; UFRJ 3048, 1 (c&s); *O. albus*: UFRJ 3892, 2; UFRJ 3894, 1 (c&s); *O. crawfordi*: UFRJ 3045, 1; UFRJ 3046, 1 (c&s); *O. cl. gilsoni*: UFRJ 3053, 19; UFRJ 3054,4 (c&s); *O. ispi*: UFRJ 3043, 13; UFRJ 3044, 4 (c&s); *O. luteus*: UFRJ 3050, 2; UFRJ 3051, 2 (c&s); *O. mulleri*: UFRJ 3049, 2; UFRJ **3895, 2 (c&s)**. **Fundulidae:** *Fundulus chrysotus*: UFRJ 3307, 6; *F. diaphanus*: UFRJ 3310, 6 ex; *F. het-*

*eroclitus*: UFRJ 33 18, 10; UFRJ 3319, 2 (c&s); *F. luciae*: UFRJ 3909, 4; UFRJ 4108, 2 (c&s); *F. majalis* UFRJ 3311, 4; UFRJ 33 11,4 (c&s); *F. notti*: UFRJ 3322, 6; *F. sciadicus*: UFRJ 3320, 10; UFRJ 3321, 2 (c&s); *Leptolucania ommata*: UFRJ 3313, 3; UFRJ 3314, 1 (c&s); *Lucania goodii*: UFRJ 330.5, 10; UFRJ 3306, 2 (c&s); *L. parva*: UFRJ 3308, 8; UFRJ **3309, 2 (c&s)**. **Goodeidae**: *Chupalichthys encaustus*: UFRJ 3299, 11; UFRJ 3300, 4 (c&s); *Characodon lateralis*: UFRJ 3303, 21; UFRJ 3304, 4 (c&s); *Crenichthys bailey*: UFRJ 3285, 7; UFRJ 3286, 3 (c&s); *Empetrichthys latos pahrump*: CAS 47063, 1 (c&s); *E. merriami*: CAS 168745, 1 (c&s); *Girardinichthys multiradiatus*: UFRJ 3287, 7; UFRJ 3288,4 (c&s); *Goodea atripinnis*: UFRJ 3291,4; UFRJ 3423, 1 (c&s); *Ilyodon whitei*: CAS 40793, 1 (c&s); *Skiffia bilineata*: UFRJ 3292, 10; UFRJ 3424, 2 (c&s); *S. lermæ*: UFRJ 3908, 8; UFRJ 4109, 2 (c&s); *Xenotoca eiseni*: UFRJ uncat., 1 (c&s); *Zoogoneticus quitzeoensis*: UFRJ 3293, 7; UFRJ 3293, 3 (c&s).

**Poeciliidae**: *Alfaro huberi*: UFRJ 3448, 6; UFRJ 3410, 4 (c&s); *Aplocheilichthys hutereaui*: UFRJ 3297, 21; UFRJ 3298,4 (c&s); *A. johnstoni*: UFRJ 3295, 11; UFRJ 3296, 4 (c&s); *A. Zamberti*: UFRJ 3887, 8; UFRJ 4105,2 (c&s); *A. normani*: UFRJ 3882,25; *A. pfaffi*: UFRJ 3884, 23; UFRJ 4106, 2 (c&s); *A. rancureli*: UFRJ 3886, 10; *A. schioetzi*: UFRJ 699, 1 (c&s); *Brachyrhuphis terrabensis*: MZUSP uncat., 1 (c&s); *Cnesterodon decemmaculatus*: UFRJ 3411, 2 (c&s); *Fluviphylaxpygmaeus*: MZUSP 29373, 63 (3 c&s); *Hypopanchax stictopleuron*: UFRJ 3875, 1; UFRJ 4106, 1 (c&s); *Limia pauciradiatu*: UFRJ 3454, 16; UFRJ 3412,4 (c&s); *L. vittata*: UFRJ 4034, 15 (3c&s); *Pamphorichthys hollandi*: UFRJ 3413, 3 (c&s); *Phalloceros caudimaculatus*: UFRJ 537, 28; UFRJ 3414, 3 (c&s); *Phalloptychus januarius*: UFRJ 3415, 4 (c&s); *Poecilia branneri*: MZUSP 42383, 2 (c&s); *P. butteri*: UFRJ 4038, 15 (3 c&s); *P. caucana*: UFRJ 4047, 25 (3 c&s); *P. chica*: UFRJ 4048, 25 (3 c&s); *P. formosa*: UFRJ 4046, 20 (2 c&s); *P. marcellinoi*: UFRJ 4043, 5; *P. latipunctatu*: UFRJ 4045, 25 (4 c&s); *P. parae*: MZUSP 42384, 2 (c&s); *P. velifera*: UFRJ 4041, 25 (3 c&s); *P. vivipara*: UFRJ 071, 27; UFRJ 3416, 2 (c&s); *Procatopus nototaenia*: UFRJ 4104, 1 (c&s); *Tomeurus gracilis*: UFRJ 3752, 268; MZUSP 42385, 3 (c&s); *Xiphophorus helleri*: UFRJ 3451, 6; UFRJ 3417, 2 (c&s); *X. variatus*: UFRJ 3418, 1 (c&s). **Profundulidae**: *Profundulus candalarius*: UFRJ 3455, 21; UFRJ 3456, 4 (c&s); *P. guatemalensis*: UFRJ 3445, 8; UFRJ 3446, 2 (c&s); *P. labialis*: UFRJ 3452, 21; UFRJ 3453, 4 (c&s). **Rivulidae**: *Austrofundulus limnaeus*: USNM 218055, 17 (2 c&s); *A. transilis*: MZUSP 38389, 4; MZUSP 38429, 1 (c&s); *Campellolebias brucei*: UFRJ 293, 6; UFRJ 1854, 2 (c&s); *C. chrysolineatus*: MZUSP 38428, 2 (c&s); UFRJ 284, 2; *C. dorsimaculatus*: UFRJ 2192, 2 (c&s); *Cynolebias adloffii*: UFRJ 4016, 12; MCP 10933, 8 (2 c&s); *C. affinis*: UFRJ 270, 11; UFRJ 271, 1 (c&s); *C. albipunctatus*: UFRJ 160, 35; UFRJ 647, 2 (all c&s); *C. alexandri*: MZUSP 38473, 2 (c&s); MNRJ 11720, 4; *C. bellottii*: MCP 11595, 5 (1 c&s); MNRJ 9753, 3; *C. carvalhoi*: MNRJ 5760, 4; *C. cinereus*: MZUSP 38504, 1 (c&s); *C. elongatus*: MNRJ 11400, 2; *C. griseus*: UFRJ 2098, 14; UFRJ 319, 1 (c&s); *C. gymnovenstris*: MZUSP 36450, 1; *C. leptocephalus*: UFRJ 687, 2; UFRJ 688, 1 (c&s); *C. luteoflammulatus*: MCP 15048, 2; *C. microphthalmus*: MZUSP 38343, 3; *C. nigripinnis*: UFRJ 2082, 1 (c&s); *C. perforatus*: UFRJ 2089, 7; UFRJ 2077, 2 (c&s); *C. porosus*: UFRJ 649, 18; UFRJ 650, 2 (c&s); *C. vanderbergi*: UFRJ 3028, 2; *C. viarius*: MCP 15050, 4 (1 c&s); *C. wolterstorffi* MZUSP 38421, 1 (c&s); MNRJ 11381, 8; *Cynopoecilus melanotuenia*: UFRJ 276, 6; UFRJ 1857, 2 (c&s); *Leptolebias aureoguttatus*: UFRJ 199, 7; UFRJ 172, 2 (c&s); *L. cruzi*: UFRJ 173, 1 (c&s); UFRJ 3678, 2 (c&s); *L. fluminensis*: UFRJ 2202, 24; UFRJ UFRJ 3679, 4 (c&s); *L. leitaoi*: UFRJ 171, 1 (c&s); *L. marmoratus*: SU(CAS) 36524, 10; *L. minimus*: UFRJ 2201,8; UFRJ 3680,4 (c&s); *L. sandrii*: MNRJ 11302,23; MZUSP 38443, 2 (all c&s); *Maratecoara formosa*: UFRJ 2112, 4; UFRJ 2111, 4 (c&s); *M. lacortei*: UFRJ 3551, 2; UFRJ 3556, 1 (c&s); *Millerichthys robustus*: UMMZ 194706, 14 (4 c&s); *Moema pepo-tei*: MUSM 3069, 6 (1 c&s); *M. piriana*: UFRJ 315, 2; MZUSP 38.515, 1 (c&s); *M. portugali*: UFRJ 262, 13; MZUSP 38512, 1 (c&s); UFRJ 283, 1 (c&s); *M. staecki*: UFRJ 317, 1 (c&s); *Neofundulus ornatipinnis*: UFRJ 2113, 1 (c&s); *N. paraguayensis*: UFRJ 3647, 17; UFRJ 3648,4 (c&s); MZUSP 36617, 1 (c&s); *N. parvipinnis*: MZUSP 36620, 5; UFRJ 267, 1 (c&s); *Pituna bitteri*: UFRJ 3031, 2; UFRJ 3171, 3 (c&s); *P. compacta*: UFRJ 2115, 2 (c&s); UFRJ 247, 21; *Plesiolebias aruana*: UFRJ 387, 15; UFRJ 3558, 5 (c&s); *P. glaucopterus*: UFRJ 3672, 6 (c&s); UFRJ 3638, 8; *P. lacerdai*: UFRJ 1156, 27; UFRJ 3558, 5 (c&s); *P. xavantei*: UFRJ 2096, 86; MZUSP 38417, 4 (c&s); *Pterolebias hoignei*: MZUSP 38391, 4; MZUSP 38439, 2 (c&s); *P. Zongipinnis*: UFRJ 3644, 9; UFRJ 3676, 2 (c&s); MZUSP 38420, 1 (c&s); UFRJ 272, 1 (c&s); *P. obliquos*: UFRJ 3034, 4; UFRJ 3035, 2 (c&s); *P. phasianus*: UFRJ 3649, 38; UFRJ 3673, 4 (all c&s); *P. peruensis*: MZUSP 38394, 1; MZUSP 38457, 1 (c&s); *P. rubrocaudatus*: MUSM 3119, 7 (1 c&s); *P. cf wischmanni*: MUSM 3116, 6 (1 c&s); *P. xiphophorus*: UFRJ 3165, 1 (c&s); *P. zonatus*: MZUSP 38392, 4; UFRJ 3166, 2 (all c&s); *Rachovia brevis*: UFRJ 295, 1 (c&s); *R. macuzipinnis*: MZUSP 38390, 3; MZUSP 38505, 1 (c&s); *R. pyropunctata*: USNM 219618, 6 (1 c&s); *Renova oscari*: UFRJ 3164, 1 (c&s); *Rivulus atratus*: MZUSP 38310, 1; MZUSP 38449, 1 (c&s); *R. bahianus*: UFRJ 3167, 46; UFRJ 277, 1 (c&s); *R. beniensis*: UFRJ 3637, 3; *R. brasiliensis*: UFRJ 3458, 32; UFRJ 3682, 2 (c&s); MZUSP 38427, 2 (c&s); *R. brunneus*: MZUSP uncat, 10; *R. caudomarginatus*: UFRJ 1806, 32; UFRJ 3683, 2 (c&s); *R. chucunaque*: USNM 293487, 68 (1 c&s); *R. cladophorus*: UFRJ 643, 4; *R. cryptocallus*: UFRJ 359, 3; UFRJ 2126, 1 (c&s); *R. cylindraceus*: USNM uncat, 2 (c&s); *R. decoratus*: UFRJ 2134, 3; UFRJ 2135, 3 (c&s); *R. depressus*: UFRJ 2118, 1 (c&s); *R. derhami*: UFRJ 392, 2 (c&s); *R. elongatus*: MZUSP 26211, 3; *R. erberi*: UFRJ 358, 3; *R. fuscolineatus*: USNM 219778, 10; *R. geayi*: INPA 2370, 6 (1 c&s); *R. haraldsiolii*: UFRJ 125, 8; *R. hartii*: MZUSP 37204, 3; MZUSP 38472, 2 (c&s); *R. hildebrandi*: USNM 92958, 1; *R. holmiae*: USNM 66302, 1; *R. immaculatus*: USNM 308411, 2; *R. janeiroensis*: UFRJ 187, 11; *R. luelingi*:UFRJ 161, 8; *R. marmoratus*: USNM 174968, 1; *R. micropus*: MZUSP 38307, 21; MZUSP 38448, 2 (c&s); *R. modestus*: UFRJ 2102, 6; UFRJ 2103, 5 (all c&s); *R. nudiventris*: MNRJ 11740, 2 (c&s); *R. ocellatus*: UFRJ 1806, 3; UFRJ 3684, 1 (c&s); *R. obscurus*: MZUSP 37208, 3; MZUSP 38440, 2 (c&s); *R. ornatus*: MZUSP 38494, 12; *R. pictus*: UFRJ 2229, 17; UFRJ 2278, 4 (c&s); *R. punctatus*: UFRJ 141, 7; UFRJ 2110, 4 (c&s); *R. rubrolineatus*: MZUSP 26371, 3; *R. santensis*: UFRJ 123,4; UFRJ 278, 1 (c&s); *R. stagnatus*: USNM 66303, 1; *R. stellifer*: UFRJ 245, 5 (c&s); *R. tecminae*: UFRJ 20858, 2; UFRJ 2095, 1 (c&s); *R. urophthalmus*: INPA 2244, 20; UFRJ 3055, 6 (c&s); *R. violaceus*: UFRJ 143, 20; UFRJ 1852, 7 (c&s); *R. zygonecetes*: UFRJ 1414, 25; UFRJ 2108, 4 (c&s); *Simpsonichthys alternatus*: UFRJ 2130, 11; UFRJ 2131, 4 (c&s); *S. antonieri*: MZUSP 38342, 29; MZUSP 38422, 1 (c&s); *S. boitonei*: UFRJ 3158, 1 (c&s); *S. bokermanni*: UFRJ 1836, 14; UFRJ 3162, 1 (c&s); *S. chacoensis*: UFRJ 3030, 1; UFRJ 3170, 1 (c&s); *S. constanciae*: UFRJ 2199, 47; UFRJ 1851, 6 (c&s); *S. costai*: UFRJ 3549, 45; UFRJ 3350,4 (all c&s); *S. flammeus*: UFRJ 2081, 116; UFRJ 280, 1 (c&s); *S. flavicaudatus*: UFRJ 2094, 24; UFRJ 3160, 4 (c&s); *S. fulminantis*: UFRJ 686, 3; UFRJ 685, 2 (c&s); *S. ghisolfi*: UFRJ 3526, 2; UFRJ 3527, 2 (c&s); *S. hellneri*: UFRJ 2093, 61; UFRJ 2080, 4 (c&s); *S. magnificus*: UFRJ 154, 12; UFRJ 260, 1 (c&s); *S.*

*multiradiatus*: UFRJ 2076, 8; UFRJ 2075, 6 (c&s); *5. myersi*: UFRJ 249, 28; UFRJ 3161, 3 (c&s); *5. notatus*: UFRJ 2068, 27; UFRJ 268, 1 (c&s); *S. stellatus*: UFRJ 2066, 5; UFRJ 2067, 4 (c&s); *S. trilineatus*: UFRJ 2133, 2; UFRJ 2132, 1 (c&s); *S. whitei*: UFRJ 2197,8; UFRJ 3159,3 (c&s); *S. zonatus*: UFRJ 142,6; UFRJ 279, 1 (c&s); *Spectrolebias semiocellatus*: UFRJ 3632, 6; UFRJ 3633, 5 (c&s); *Stenolebias bellus*: UFRJ 386, 1 (c&s); *S. damascenoi*: MZUSP 41392, 2 (c&s); *Terranatos dolichopterus*: USNM 219618, 25 (2 c&s); *Trigonectes aplocheiloides*: USNM 230033, 1; *T. balzanii*: UFRJ 3677, 18; UFRJ 3671, 6 (c&s); *T. macrophthalmus*: MZUSP 38453, 1 (c&s); *T. rogoaguae*: CAS 42532, 20; *T. rubromarginatus*: UFRJ 3553, 13; UFRJ 3554, 3 (c&s); *T. strigabundus*: UFRJ 2100, 31; UFRJ 2114, 2 (c&s). **Valenciidae**: *Valencia hispanica*: AMNH 38401,2; AMNH 38432, 3 (1 c&s).

**Non-Cyprinodontiformes - Atherinidae**: *Atherinosoma ogilbyi*: UFRJ 4154, 3; UFRJ 4155, 2(c&s); *Craterocephalus honoriae*: UFRJ 4164, 1; UFRJ 4165, 2 (c&s). **Atherhopsidae**: *Atherinella brasiliensis*: UFRJ 022, 2 (c&s). **Hemirhamphidae**: *Hyporhamphus unitaeniatus*: UFRJ 3284, 2; UFRJ 4115, 1 (c&s). **Melanotaeniidae**: *Melanotaenia affinis*: UFRJ 4166, 2; UFRJ 4167, 2 (c&s); *M. duboulayi*: UFRJ 4156, 2; UFRJ 4172, 2(c&s); *Melanotaenia* sp.: UFRJ 4112, 2 (c&s); *Melanotaenia* sp.: UFRJ 4113, 1 (c&s); *Pseudomugil gertrudae*: UFRJ 4162, 1; UFRJ 4163, 1 (c&s); *P. signifer*: UFRJ 4158, 4; UFRJ 4159, 2 (c&s); *Rhadinocentrus ornatus*: UFRJ 4160, 3; UFRJ 4161, 2 (c&s). **Telmatherinidae**: *Telmatherina ladigesi*: UFRJ 4114, 1 (c&s).

### Appendix B

Data matrix of 106 characters used in the phylogenetic analysis of the Cyprinodontiformes. Character and character state numbers are according to those presented in the text. “P” indicates polymorphic taxa and “?” character states not pertinent. Families are ordered according to Parenti (1981).

	1-5	6-10	11-15	16-20	21-25	26-30	31-35	36-40	41-45	46-50	51-55	56-60
Outgroup	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000
Rivulidae	10020	00000	00100	00000	00100	10100	01001	11000	00110	10010	01000	11011
Aplocheilidae	10010	00000	00101	00000	01100	10000	01001	01000	00100	10010	01000	01011
Profundulidae	2?000	01101	10110	00010	00000	11000	01110	01000	10011	00100	00100	00100
Fundulidae	2?001	01111	01110	01010	00000	11010	01010	011?0	10011	01101	00001	00100
Valenciidae	00000	00121	00110	00010	00000	11010	01010	01001	10011	00100	10001	00100
Poeciliidae	01000	10121	00110	10111	-10010	110P0	11010	010P0	11011	00100	00001	00100
Anablepidae	01000	10121	00110	10111	10001	11020	01010	01010	10011	00100	00101	00100
Goodeidae	2?000	01111	10110	PO010	00000	11001	01110	01000	10011	00P00	00010	00100
Cyprinodontidae	01100	00121	00110	10010	00000	11020	01010	01010	10011	00100	00001	00100

	61-65	66-70	71-75	76-80	81-85	86-90	91-95	96-100	101-105	106
Outgroup	00000	00000	00000	00000	00000	00000	00000	00000	00000	0
Rivulidae	01300	10011	02210	01?00	00110	11011	20111	01102	01112	1
Aplocheilidae	01200	10001	01110	10100	00110	11010	10111	00102	00102	1
Profundulidae	10100	00000	10011	00110	00010	11100	00001	10001	10001	0
Fundulidae	00000	00000	10010	00101	10010	11100	00001	10000	10001	0
Valenciidae	00000	00001	10010	00100	00010	11100	00001	10000	00001	0
Poeciliidae	00010	00001	10000	00100	00011	11100	00001	10010	00001	0
Anablepidae	00010	00101	10010	00100	00010	11000	00001	10000	10001	0
Goodeidae	00001	01000	10011	00110	00010	11100	00001	10000	10001	0
Cyprinodontidae	00010	01001	10010	00100	01011	11100	11001	10000	00001	0