



## Phylogenetic position and taxonomic status of *Anablepsoides*, *Atlantirivulus*, *Cynodonichthys*, *Laimosemion* and *Melanorivulus* (Cyprinodontiformes: Rivulidae)

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A maximum parsimony analysis of a combined set of mitochondrial and morphological data available in the literature for 33 rivuline taxa and three outgroups confirms *Rivulus* as a paraphyletic assemblage. In order to adjust a generic classification to our present phylogenetic knowledge on rivuline relationships, the following taxonomic changes are proposed: *Rivulus*, restricted to two species endemic to Cuba, is hypothesized to be the most basal rivuline lineage, distinguished from all other non-annual rivulines by having all hypurals fused into a single plate, neural prezygapophysis of caudal vertebrae rudimentary, fourth ceratobranchial teeth absent, about 50 % of the anterior portion of the caudal fin covered by scales, four neuromasts on the anterior supraorbital series, and a black round spot with white margin on the dorsoposterior portion of the caudal peduncle in females; *Anablepsoides*, *Atlantirivulus*, *Laimosemion*, *Melanorivulus* and *Cynodonichthys*, previously classified as subgenera of *Rivulus*, are considered as valid genera; *Laimosemion*, including 24 species from northern South America, constitutes the sister group to a clade comprising *Melanorivulus*, *Cynodonichthys*, *Anablepsoides*, *Atlantirivulus*, and all annual rivuline genera, which is supported by a well-developed dorsal process of the urohyal and an expanded lateral articular facet of the first hypobranchial; *Melanorivulus*, comprising 34 species from central and northeastern South America, *Cynodonichthys* with 27 species from Central America and Trans-Andean South America, *Anablepsoides* with 42 species from northern and northeastern South America and Smaller Antilles, and *Atlantirivulus*, with 11 species endemic to the eastern Brazilian coastal plains are diagnosed by combinations of morphological characters, including osteology, cephalic laterosensory system and colour patterns.

### Introduction

The cyprinodontiform family Rivulidae is a diversified group of killifishes, with about 350 valid species occurring between southern Florida and northeastern Argentina. Rivulids typically inhabit shallow swamps and streams, but each species exhibit a strong preference for specific

habitats, usually restricted to either forests or savannahs (e.g., Costa, 2009a). Great part of the rivulid taxa, known as annual killifishes, are uniquely found in swamps and isolated pools that seasonally dry. The ability to survive in seasonal swamps and pools is due to the thickened chorion eggs, which make eggs resistant to water loss, and a complex embryonic development,

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including diapause (e.g., Wourms, 1972), as well as elaborated sexual behaviour (e.g., Belote & Costa, 2002, 2003). In contrast, the remaining rivulids are only found in perennial streams and are consequently known as non-annual killifishes.

Costa (1990a–b) first formally divided the Rivulidae into two subfamilies: the Rivulinae, comprising the non-annual killifish genus *Rivulus* and some annual killifish genera (e.g., *Pterolebias*, *Trigonectes*, *Neofundulus*); and, the Cynolebiasinae, including *Cynolebias* and other closely related annual killifish genera. Subsequent phylogenetic studies confirmed morphological and molecular

support for this basic classificatory scheme with some adjustments, including the transference of some annual killifish genera (e.g., *Terranatos* and *Plesiolebias*) from the Cynolebiasinae to the Rivulinae (Costa, 1998; Hrbek & Larson, 1999; Murphy et al., 1999), and the transfer of a group of *Rivulus* to the genus *Kryptolebias* belonging to its own subfamily (Costa, 2004a).

The Rivulinae presently comprises 17 annual killifish genera (*Aphyolebias*, *Austrofundulus*, *Gnatholebias*, *Llanolebias*, *Maratecoara*, *Micromoema*, *Moema*, *Neofundulus*, *Papiliolebias*, *Pituna*, *Plesiolebias*, *Pterolebias*, *Rachovia*, *Renova*, *Stenolebias*, *Terranatos*, *Trigonectes*), which have been sup-

**Table 1.** Data matrix of distribution of character states of 116 morphological characters among 36 aplocheiloid taxa. Characters and included states are according to Appendix 1.

<i>Scriptaphyosemion geryi</i>	01000 00010	00000 00000	00000 00000	00000 00000	00000 10000
<i>Kryptolebias ocellatus</i>	11000 00111	11111 00010	00000 01000	00020 01000	00001 00001
<i>Nematolebias whitei</i>	10000 10011	11111 02111	00000 01100	10011 01000	01000 1000–
<i>Rivulus cylindraceus</i>	10000 10111	11111 00010	10000 01000	11011 01011	11001 00001
<i>Laimosemion strigatus</i>	11000 00111	11111 00010	10000 01000	11010 01011	11001 10001
<i>Laimosemion geayi</i>	11000 00111	11111 00010	10000 01000	11010 01011	11001 10001
<i>Laimosemion xiphidius</i>	11000 00111	11111 00010	10000 01000	11010 01011	11001 10001
<i>Laimosemion amanapira</i>	10000 00111	11111 00010	10000 01100	11010 01011	11001 10001
<i>Cynodonichthys tenuis</i>	10000 00111	11111 00010	10000 01000	11011 01011	11001 00101
<i>Cynodonichthys magdalenae</i>	10000 00111	11111 00010	10000 01000	11011 01011	11001 00101
<i>Anablepsoides amphoreus</i>	10000 00111	11111 00010	10010 01000	11021 11011	11101 01101
<i>Anablepsoides stagnatus</i>	10000 00111	11111 10010	10010 01000	11021 11011	11101 01101
<i>Atlantirivulus janeiroensis</i>	10000 00111	11111 00010	10100 01000	11011 11011	11001 01101
<i>Atlantirivulus santensis</i>	10000 00111	11111 00010	10100 01000	11011 11011	11001 01101
<i>Atlantirivulus luelingi</i>	10000 00111	11111 00010	10100 01000	11011 11011	11001 01101
<i>Melanorivulus punctatus</i>	10000 10111	11111 00010	11000 01100	11011 01111	11101 10101
<i>Melanorivulus crixas</i>	10000 10111	11111 00010	11000 01100	11011 01111	11101 10101
<i>Melanorivulus apiamicci</i>	10000 10111	11111 00010	11000 01100	11011 01111	11101 10101
<i>Pituna poranga</i>	10101 00111	01111 00010	1100? 01100	11011 11111	01001 01101
<i>Maratecoara lacortei</i>	10101 00111	01111 00010	11001 01100	11011 11111	01001 01100
<i>Papiliolebias bitteri</i>	10101 00111	01111 00010	11001 01100	11111 11111	11001 01101
<i>Plesiolebias aruana</i>	10101 12111	01111 00010	11001 01100	11111 01111	01001 01101
<i>Trigonectes rubromarginatus</i>	10000 00101	11111 00010	10010 01010	11011 11011	11001 00101
<i>Trigonectes balzani</i>	10000 00101	11111 00010	10010 01010	11011 11011	11001 00101
<i>Neofundulus paraguayensis</i>	10000 00111	11111 00010	10010 01010	11011 11011	11001 00101
<i>Pterolebias longipinnis</i>	10000 01111	11111 11010	10010 01000	11111 11011	11011 01101
<i>Pterolebias phasianus</i>	10000 01111	11111 11010	10010 01000	11111 11011	11011 01101
<i>Gnatholebias zonatus</i>	10000 01111	11110 01110	10010 01000	11011 11011	11001 11111
<i>Rachovia maculipinnis</i>	10100 01111	11110 01110	10010 11000	11011 11011	11011 01111
<i>Austrofundulus limnaeus</i>	10010 01111	11110 00010	10010 11000	11011 11011	11001 01111
<i>Terranatos dolichopterus</i>	10010 12111	11010 00011	10010 01000	11011 01011	11001 01111
<i>Renova oscari</i>	10000 01111	11111 00010	10010 01000	11011 11011	11001 01111
<i>Micromoema xiphophora</i>	10000 00111	11111 11010	10010 01000	11011 11011	11001 01111
<i>Moema piriana</i>	10000 01111	11111 00010	10010 01001	11011 11011	11001 00101
<i>Moema staecki</i>	10000 01111	11111 01010	10010 01001	11011 11011	11001 00101
<i>Aphyolebias peruensis</i>	10000 01111	11110 01010	10010 01001	11011 11011	11001 00101



ported both by morphology and mitochondrial (mt-)DNA phylogenies (e. g., Costa, 1998; Hrbek & Larson, 1999; Murphy et al., 1999). In contrast, monophyly of *Rivulus* has not been supported by mt-DNA phylogenies (e. g., Hrbek & Larson, 1999; Murphy et al., 1999; Vermeulen & Hrbek, 2005), whereas morphological studies weakly support monophyly (Costa, 2006a). In all mt-DNA phylogenies, species of *Rivulus* are grouped into distinct paraphyletic lineages, each corresponding to informal species groups or subgenera delimited by morphology (Huber, 1992, 1999; Costa, 1998, 2006a, 2008a). In morphology-based phylogenies, no unambiguous character state supporting *Rivulus* was found (Costa, 1998, 2006a), but unique morphological character states have supported assemblages formally recognized as sub-

genera, which often exhibit specialized ecological preferences (Costa, 2006a).

While the taxonomic status of *Rivulus* remains uncertain, after continuous efforts directed to sample non-annual rivulid killifishes in their specific biotopes, the number of described species has continuously increased in recent years. Lazara (1984) reported 55 valid species of *Rivulus* excluding those later transferred to other genera, but today 135 valid species are placed in *Rivulus*. However, the higher number of taxa available and more detailed morphological studies involving rivulines (e. g., Costa, 2005a, 2011) have not been enough to find characters supporting *Rivulus* as a monophyletic unit. The objective of this study is to combine available data on morphology and mt-DNA into a single analysis in order

00-00 00000	00000 00000	00000 00000	00000 00000	00000 00000	00000 00000	00000 00011	00000 0
11001 01010	00000 10010	01101 00000	00000 00000	00010 00000	00000 10000	00000 10000	00100 0
11001 01010	10010 11010	00001 00110	00000 1000?	20011 -0010	00000 00000	00000 00000	00000 0
11001 01011	10000 11010	11101 11000	00100 00011	00010 01000	01000 00000	01000 00000	00100 0
11001 01111	00010 11010	11103 11000	00000 00000	00010 31000	01000 00001	00001 00001	00001 0
11001 01111	00010 11010	11101 11000	00000 00000	00010 31000	01000 00001	00001 00001	00001 0
11001 01011	00010 11010	11101 11000	00100 00000	00010 30000	01000 00000	00000 00000	00000 0
11001 01011	00010 11010	11104 11000	00000 00000	00010 30000	00000 00000	00000 00000	00001 0
11001 01011	00000 11010	11101 10000	00000 00000	00010 00000	00100 00010	00010 00010	00010 0
11001 01011	00000 11010	11101 10000	00000 00000	00010 00000	00100 00000	00010 00000	00010 0
11011 01011	00000 11010	12101 10000	00100 00000	00010 00000	00000 00000	00000 00000	00010 0
11011 01011	00000 11010	12101 10000	00100 00000	00010 00000	00010 00000	00010 00000	00010 0
11001 01011	00010 11010	11101 11000	00000 00000	01010 00000	01000 00000	00010 00000	00010 0
11001 01011	00010 11010	11101 11000	00000 00000	01010 00000	01000 00000	00010 00000	00010 0
11001 01011	00010 11010	11101 11000	00000 00000	01010 00000	01000 00000	00010 00000	00010 0
11001 01011	00010 11010	11101 11000	00000 00000	01010 00000	01000 00000	00010 00000	00010 0
11001 01110	00010 11010	11103 10000	00100 00000	00010 00000	01000 00001	00010 00001	00010 1
11001 01110	00010 11010	11103 10000	00100 00000	00010 00000	01000 00001	00010 00001	00010 1
11001 01110	00010 11010	11101 10000	00100 00000	00010 30000	01000 00001	00010 00001	00010 1
11101 11010	11110 11111	11103 11000	00100 00012	10111 11011	10001 10000	10000 10000	10000 0
11101 01010	11110 11011	11003 11000	00200 00102	10111 10011	00001 00000	00000 00000	00000 0
11101 11010	11100 11011	11103 11000	00300 00002	10211 11011	10000 10000	00000 10000	00000 0
11101 ?1010	11110 11011	11000 11000	00100 00002	20110 10010	00000 10000	00000 10000	00000 0
11011 01011	00001 11010	11102 10000	10100 00011	00110 20010	00000 01000	00000 01000	01000 0
11011 01011	00001 11010	11101 10000	10100 00011	00?10 10010	00000 01000	00000 01000	01000 0
11011 01011	00001 11010	11101 10000	00100 00011	00010 10010	00000 00000	00000 00000	01000 0
11011 01011	01001 11110	11101 10000	11210 11100	00010 10110	00000 00000	00000 00000	10000 0
11011 01011	01001 11110	11101 10000	11210 11100	00010 10110	01000 01000	00000 01000	10000 0
11011 01011	11001 11110	11113 10001	11210 11100	00010 10010	00000 00000	00000 00000	00000 0
11011 11011	11001 11110	11113 10010	00200 11110	00010 00011	00000 01000	00000 01000	00000 0
11001 11011	10001 11010	1121? 11100	00101 11012	00010 10011	00000 00000	00000 00000	00000 0
11001 11011	11011 11010	11211 00100	10201 11102	00010 10011	00000 00000	00000 00000	00000 0
11011 01011	01001 11110	11111 11001	00100 11000	00010 10010	00000 00000	00000 00000	00010 0
11011 11011	00011 11110	11111 11001	00100 11100	00010 10010	00000 00010	00000 00010	00000 0
11011 01011	00001 11110	11111 10001	00100 11100	00010 10010	00000 01010	00000 01010	00000 0
11011 11011	00001 11110	11112 11001	00100 11100	00010 10010	00000 00100	00000 00100	00000 0
11011 11011	00001 11010	11111 10001	0010? 11100	00010 10010	00000 00100	00000 00100	00000 0



to find the best generic classification compatible with our present phylogenetic knowledge on rivuline killifishes.

### Material and methods

Morphological characters were studied in hundreds of specimens belonging to about 150 rivuline species, including 83 species of *Rivulus*, as listed in Costa (1998, 2003a–g, 2004a–e, 2005a–b, 2006a–b, 2007a–g, 2008b–f, 2009b, 2010a–b, 2011), Costa & Brasil (2008), Costa & Lazzarotto (2008), Costa & De Luca (2009, 2011a–b), Costa & Lanés (2009) and Costa & Vono (2009); specimens were fixed in formalin immediately after collection, for a period of about 10 days, and then transferred to ethanol 70 %. Most material is deposited in the ichthyological collection of the Instituto de Biologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro (UFRJ). Morphological characters studied in all this material included osteology, laterosensory system and other cephalic structures, fin morphology and colour patterns. The phylogenetic position of the remaining rivuline species was also inferred from the characters described and illustrated in the taxonomic literature. Osteological preparations (c&s) were made according to Taylor & Van Dyke (1985). Terminology for frontal squamation followed Hoedeman (1958) and for cephalic neuromast series Costa (2001).

The phylogenetic analysis was based on the combination of morphological characters described in previous studies (Costa, 1990a, 1998, 2004a, 2005a, 2011) and GenBank mt-DNA sequences originally used by Murphy et al. (1999). Therefore terminal taxa included in the analysis (Table 1) are those representing all the main rivuline lineages with data available both for morphology and mt-DNA. In order to represent the maximum number of lineages in the analysis, molecular data for an undescribed species (“*Rivulus* sp. Tobogon”) were mixed to morphological data of *R. amanapira*, a similar, closely related species. Identification of the species analysed by Murphy et al. (1999) as *R. caudomarginatus* and *R. violaceus* were corrected to *Kryptolebias ocellatus* and *R. crixas*, respectively. Three outgroup taxa were included: the nothobranchiid *Scriptaphyosemion geryi*, the kryptolebiasine *Kryptolebias ocellatus*, and the cynolebiasine *Nematolebias whitei*.

Character statements for morphology were formulated according to Sereno (2007). Colour patterns when consistently identified (i.e., all specimens of two or more terminal taxa sharing a similar colour pattern, composed of one or more colours, at the same position of a morphological structure) were treated as independent characters. Characters showing high levels of subjectivity in character state delimitation among the numerous terminal taxa (e.g., dorsal and anal fin morphology, flank colour patterns in males) were excluded from the analysis. All characters were treated as unordered and are listed in Appendix 1. Distribution of character states of morphological characters among terminal taxa appears in Table 1.

The molecular analysis included sequences of the mitochondrial genes cytochrome c oxidase I, 12S rRNA and 16S rRNA; protocols for extraction, amplification and sequencing are described in Murphy & Collier (1996, 1997) and Murphy et al. (1999); GenBank accession numbers are provided in Murphy et al. (1999). Sequences were aligned using Clustal-W (Chenna et al., 2003) and subsequently optimized manually. All genes were analysed giving equal weight to all sites. The small cytochrome b segment also used by Murphy et al. (1999) was not included in the present study by showing high levels of saturation at the third position and being problematic for some rivulid taxa (e.g., Murphy et al., 1999), resulting in terminal taxa reduction and possible inaccurate data. The search for most parsimonious tree (traditional search), bootstrap analysis (1000 replicates), and distribution of synapomorphies among nodes were performed with TNT 1.1 (Goloboff, Farris & Nixon, 2008).

### Results and discussion

Among the 116 morphological characters analysed, 111 were parsimony-informative. The alignment for the segments of the mitochondrial genes sampled determined 1311 sites, among which 622 were parsimony-informative, whereas 531 were constant and 158 were variable but not parsimony-informative. The combined analysis of morphological and molecular data into a single matrix generated a single most parsimonious cladogram (tree length: 4687; consistency index excluding non-informative characters: 0.30; retention index: 0.43) (Fig. 1), where different assem-

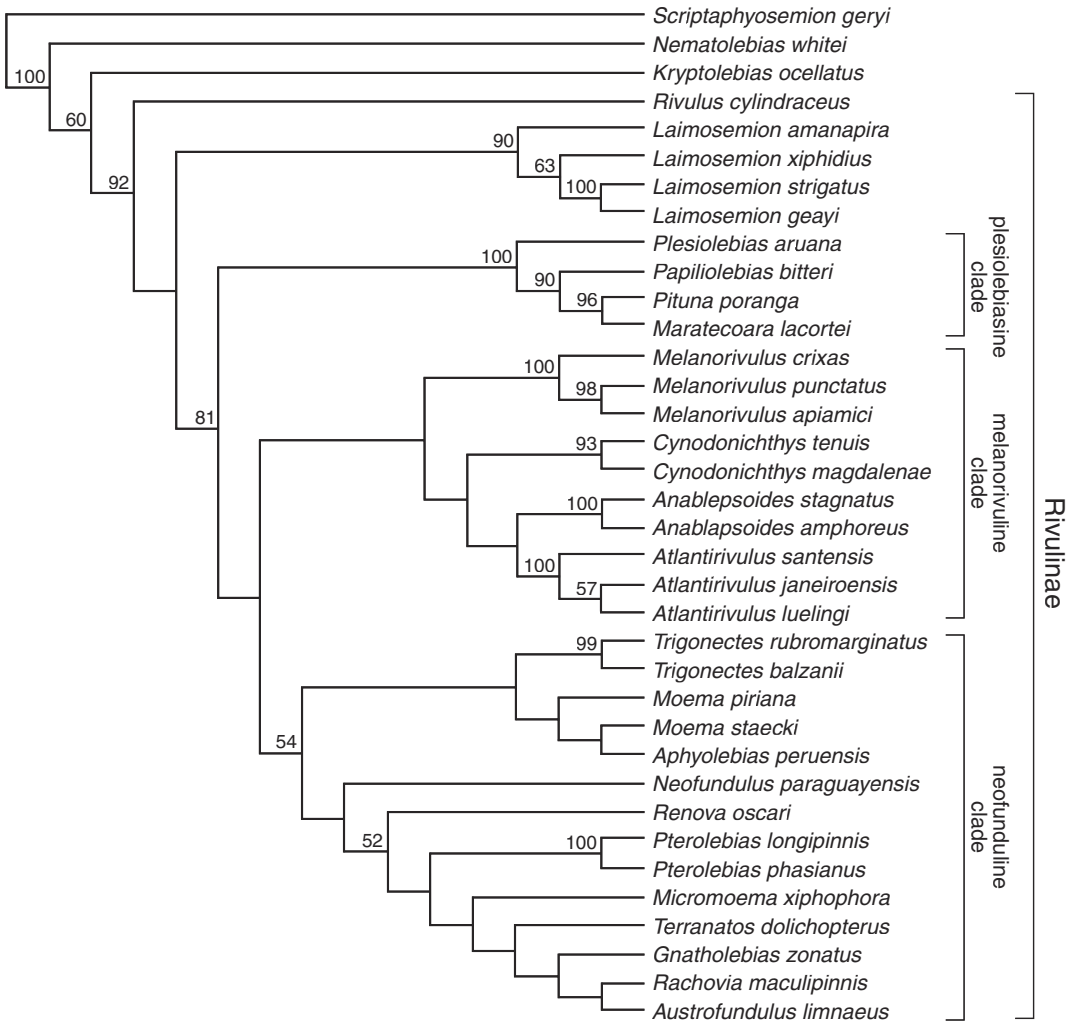


Fig. 1. Most parsimonious tree from the combined analysis of morphological and mt-DNA characters. Numbers above the base of a node are bootstrap percentages higher than 50 %.

blages of *Rivulus*, which correspond to formally recognized subgenera, appear as well-supported independent paraphyletic lineages. In order to establish a generic rivuline classification consistent with the present analyses and previous studies (e.g., Murphy et al., 1999; Hrbek & Larson, 1999), former subgenera of *Rivulus* are herein elevated to genera as discussed below.

Monophyly of the Rivulinae is strongly supported, being diagnosed by eight morphological synapomorphies: ventral process of the angulo-articular narrow, about triangular (21.1), interhyal rudimentary or absent (32.1), first epibranchial twisted (39.1), subdistal process of the

second epibranchial absent (40.1), uncinat process of the third epibranchial forming an angle of about 45–60° (41.1), anteriorly directed paired process on the first vertebra (60.1; reversed in plesiolebiasines and *Melanorivulus*); membrane between preopercular laterosensory series and isthmus continuous (71.1), and E-scales not overlapped (76.1). *Rivulus cylindraceus*, the type species of the genus, endemic to Cuba, appears as the sister group to all other rivulines, a hypothesis already consistently postulated by authors analyzing mt-DNA alone (e.g., Murphy et al., 1999; Hrbek & Larson, 1999), but not supported by any morphological character. On the other hand, no



morphological character unambiguously support close relationships between *R. cylindraceus* and the other rivuline lineages historically placed in *Rivulus*. As a consequence of the total evidence hypothesis, the genus *Rivulus* should be restricted to include only the type species and a closely related species, *R. insulaepinorum*, also endemic to Cuba and exhibiting similar derived external morphological features (de la Cruz & Dubitsky, 1976).

More strongly supported is the sister group relationship between a clade formed by species placed in the subgenera *Laimosemion* and *Owiyeye* (Costa, 2006a), and a clade comprising all other rivulines except *Rivulus sensu stricto*, as also supported in previous molecular analyses (e.g., Murphy et al., 1999; Hrbek & Larson, 1999). The latter clade is well-supported by bootstrap values, and is morphologically diagnosed by the presence of a cartilage extending on the entire lateral part of the first hypobranchial (48.1). This derived condition differs from that in *Kryptolebias* and nothobranchiids, in which the first hypobranchial is a slender bone curved laterally, with the lateral cartilage restricted to the articular zone to the first ceratobranchial (Costa, 2004a: fig. 4a). In *Rivulus* and *Laimosemion*, the lateral part of the first hypobranchial is widened, having a separate minute cartilage on the anterolateral margin of the bone, but the lateral cartilage is restricted to the articular zone, as occurring in *Kryptolebias*, thus differing from the apomorphic extended cartilage (Costa, 2004a: fig. 4b).

Species placed in *Melanorivulus*, *Cynodonichthys*, *Anablepsoides*, and *Atlantirivulus* (Huber, 1999; Costa, 2006a, 2008a) form a weakly-supported clade (hereafter termed melanorivuline clade), the sister group of a clade comprising the genera *Aphyolebias*, *Austrofundulus*, *Gnatholebias*, *Micromoema*, *Moema*, *Neofundulus*, *Pterolebias*, *Rachovia*, *Renova*, *Terranatos*, and *Trigonectes* (hereafter termed neofunduline clade). The former clade is morphologically diagnosed by the presence of a small rounded black spot on the dorsal portion of the caudal-fin base in females, with a white dot on the anterior margin (114.1). This colour pattern differs from the female caudal ocellus occurring in *Rivulus*, in which the large round black spot has a white margin and is placed on the end of the caudal peduncle instead of on the membranous part of the caudal fin. However, in females of several species of *Anablepsoides* (i.e., *R. igneus* and closely related species) that caudal

spot on the caudal fin is absent. In addition, the plesiolebiasine clade (Costa, 2011) is hypothesized as the sister group to the melanorivuline plus neofunduline clade (Fig. 1).

The melanorivuline clade is also supported in the molecular study by Murphy et al. (1999: fig. 4), but not by Hrbek & Larson (1999: fig. 4), where *Melanorivulus* alone is placed as the sister group to the neofunduline clade, and *Atlantirivulus* appears as the sister group to the clade including *Cynodonichthys*, *Anablepsoides*, *Melanorivulus* and the neofunduline clade, nor in Vermeulen & Hrbek (2005: fig. 9), where *Anablepsoides* alone is the sister group to the neofunduline clade, and *Atlantirivulus* is the sister group to the plesiolebiasine clade. Those rivuline relationships proposed by Hrbek & Larson (1999) and Vermeulen & Hrbek (2005) are not supported by any morphological character. Diagnostic features for independent lineages formerly placed in *Rivulus* are listed and discussed below.

## Taxonomic accounts

### *Rivulus* Poey, 1860

*Rivulus* Poey, 1860: 299 (type species: *Rivulus cylindraceus* Poey, 1860; type by monotypy; gender masculine).

**Diagnosis.** *Rivulus* comprises medium-size species reaching about 50 mm SL, with dark colours in males and short and rounded fins in both sexes. It is distinguished from all other genera of non-annual rivulines by the following apomorphic character states: all hypurals fused to compose a single plate (vs. separated by middle gap); neural prezygapophysis of caudal vertebrae rudimentary (vs. well developed); fourth ceratobranchial teeth absent (vs. present); about 50 % of anterior portion of caudal fin covered by scales (vs. scales restricted to the basal portion of the fin); four neuromasts on the anterior supraorbital series (vs. three); black round spot with white margin on the dorsoposterior portion of caudal peduncle in females (vs. a rounded black spot with small white spot on anterior, sometimes on the dorsal part of the caudal fin base, when marks are present). Another apomorphic condition shared by species of *Rivulus* is a blue humeral blotch in males, but a similar colour pattern is also found in some species of *Laimosemion*.





**Included species.** *Rivulus cylindraceus* Poey, 1860 and *R. insularinorum* Cruz & Dubitsky, 1976.

**Remarks.** *Rivulus* is herein restricted to two species endemic to Cuba, which are hypothesized to comprise the sister group to a clade comprising all other rivulines (Fig. 1). “*Rivulus*” *roloffi* Roloff, 1938 from the Caribbean island of Hispaniola, Dominican Republic, considered as closely related to *R. cylindraceus* by Huber (1992), is herein not included in the genus. Molecular studies have indicated it as being more closely related to other rivulines than to *R. cylindraceus* (Murphy et al., 1999; Hrbek & Larson, 1999), but preserved material for morphological studies was not available for the present analysis. As presently it is not possible to assign “*Rivulus*” *roloffi* to any genus, it is kept as an incertae sedis rivuline species, until a complete set of morphological and molecular data can be analysed.

**Distribution.** Cuba.

**Habitat.** Species of *Rivulus* are found in rivers and swamps, both along coastal plains (de la Cruz & Dubitsky, 1976; pers. obs.) and mountains (Hoedeman, 1958). In the Llanura de Zapata (western Cuba), *R. cylindraceus* is found in still waters, about 30–40 cm deep, sympatric with poeciliids and the cyprinodontid *Cubanichthys cubensis* (pers. obs.).

#### ***Laimosemion* Huber, 1999**

*Laimosemion* Huber, 1999: 49 (first proposed as a subgenus of *Rivulus* Poey; type species: *Rivulus geayi* Vaillant, 1899; type by original designation; gender masculine).

*Owiyeye* Costa, 2006a: 156 (first proposed as a subgenus of *Rivulus* Poey; type species: *Rivulus amanapira* Costa, 2004; type by original designation; gender masculine).

**Diagnosis.** *Laimosemion* comprises a diversified clade of killifishes, containing both small species with no more than 20 mm SL as the maximum adult size and medium sized species reaching between about 30 and 40 mm SL, exhibiting a great diversity of colour patterns. Fin morphology is greatly variable among species: caudal fin is usually truncate or subtruncate, but may be rounded or lyre-shaped; dorsal and anal fins are

often short, rounded or slightly pointed, but may be long, reaching the middle of the caudal fin; and, pelvic fins are commonly short as in other non-annual rivulines, but may be long, with filamentous extensions.

*Laimosemion* differs from *Rivulus* by having the caudal-fin squamation not surpassing the basal portion of the fin (vs. reaching the middle of the fin), three neuromasts on the anterior supraorbital series (vs. four), presence of teeth on the fourth ceratobranchial (vs. absence), absence of a black round spot with white margin on the dorsoposterior portion of caudal peduncle in females (vs. presence), dorsal hypural plate separated from ventral hypural plate by a middle gap (vs. dorsal and ventral plates fused), and neural prezygapophysis of caudal vertebrae well-developed (vs. rudimentary).

*Laimosemion* is distinguished from *Melanorivulus*, *Cynodonichthys*, *Anablepsoides*, and *Atlantirivulus* by having the lateral cartilaginous portion of the first hypobranchial restricted to articulation area (vs. dorsally expanded). *Laimosemion* is also distinguished from *Melanorivulus* by the margins of the unpaired fins not being distinctively black pigmented in females (vs. black pigmentation concentrated on the whole margin of the caudal fin and on the distal margin of the dorsal and anal fins); from *Anablepsoides* by the absence of scales on the chin (vs. presence); and, from *Atlantirivulus* by having the neuromasts of the infraorbital series aligned around the eye (vs. arranged in zigzag row) and by having a straight ventral process of the angulo-articular (vs. curved). It is also distinguished from *Cynodonichthys* and *Anablepsoides* by the absence of the ventral process of the posttemporal. In addition, most species of *Laimosemion* differs from all other rivulines by the intense yellow or orange pigmentation of the anal fin in adult females (vs. hyaline, sometimes pale pink in *Atlantirivulus*).

**Included species.** *Laimosemion agillae* (Hoedeman, 1954), *L. altivelis* (Huber, 1992), *L. amanapira* (Costa, 2004), *L. dibaphus* (Myers, 1927), *L. breviceps* (Eigenmann, 1909), *L. cladophorus* (Huber, 1991), *L. corpulentus* (Thomerson & Taphorn, 1993), *L. frenatus* (Eigenmann, 1912), *L. geayi* (Vaillant, 1899), *L. gransabanae* (Lasso, Taphorn & Thomerson, 1992), *L. kirovskiyi* (Costa, 2004), *L. lyricauda* (Thomerson, Berkenkamp & Taphorn, 1991), *L. mahdiaensis* (Suijker & Collier, 2006), *L. manaensis* (Hoedeman, 1961), *L. nicoi* (Thomerson &



Taphorn, 1992), *L. rectocaudatus* (Fels & de Rham, 1981), *L. romeri* (Costa, 2003), *L. sape* (Lasso-Alcalá, Taphorn, Lasso & León-Mata, 2006), *L. strigatus* (Regan, 1912), *L. tecminae* (Thomerson, Nico & Taphorn, 1992), *L. torrenticola* (Vermeulen & Isbrücker, 2000), *L. uakti* (Costa, 2004), *L. uatuman* (Costa, 2004), *L. xiphidius* (Huber, 1979).

**Remarks.** Species herein included in *Laimosemion* were placed in two subgenera of *Rivulus* by Costa (2006a): *Laimosemion* diagnosed by the epipleural ribs being bifid, and *Owiyeje* diagnosed by the absence of dermosphenotic bone, frontal scales transversely arranged, and a transverse stripe through chin. However, although the presence of epipleural ribs being unique among rivulids, the distribution of this condition is poorly documented among species of *Laimosemion*. Since all phylogenetic analysis using mt-DNA support species of *Laimosemion* and *Owiyeje* as members of a single lineage (Murphy et al., 1999; Hrbek & Larson, 1999; Hrbek et al., 2004; Vermeulen & Hrbek, 2005), the latter assemblage is herein considered as a synonym of *Laimosemion*.

**Distribution.** North-western South America; central and eastern Brazilian Amazon; river basins of Guianas; upper Orinoco River basin in Venezuela and Colombia; Rio Negro basin in Brazil; and lower Peruvian Amazon.

**Habitat.** Species of *Laimosemion* are found in different kinds of habitat. *Laimosemion strigatus* and closely related species (e.g., *L. geayi* and *L. dibaphus*) are usually found in the marginal places of clear water streams with sandy bottom, placed within dense forests (Costa, 2006a). *Laimosemion torrenticola* and *L. gransabanae* are found in the shallow streams among rocks of the highland savannahs of the central part of the Guiana Shield (Lasso et al., 1992; Vermeulen & Isbrücker, 2000). *Laimosemion amanapira* and closely related species (e.g., *L. rectocaudatus* and *L. tecminae*), are usually found in shallow, black-water isolated pools, about 10–15 cm deep, with bottom covered by thick layer of litter, both in forests and open savannahs (Fels & de Rham, 1982; Thomerson et al., 1992; Costa, 2004b–c; Lasso-Alcalá et al., 2006; Suijker & Collier, 2006).

### *Melanorivulus* Costa, 2006

*Melanorivulus* Costa, 2006: 161 (first proposed as a subgenus of *Rivulus* Poey; type species: *Rivulus punctatus* Boulenger, 1895; type by original designation; gender masculine).

**Diagnosis.** *Melanorivulus* includes small to medium-sized species, reaching between about 20 and 40 mm SL, typically having short fins and red dots arranged to form chevron-like marks on the flank. *Melanorivulus* is distinguished from all other rivuline genera by the presence of black pigmentation concentrated on the whole margin of the caudal fin and on the distal margin of the dorsal and anal fins in females (vs. never a similar colour pattern). Other apomorphic diagnostic character states supporting monophyly of *Melanorivulus*, but homoplastically occurring in other rivuline genera, are: ventral process of the angulo-articular minute (also occurring in plesiolebiasines; vs. process well-developed), dorsal arm of preopercle pointed, dorsal segment of preopercular canal absent (also occurring in plesiolebiasines, cynolebiasines and most species of *Laimosemion*; vs. dorsal arm of preopercle truncate, dorsal segment of preopercular canal present), and vomerine teeth absent (vs. teeth present; also absent in most species of *Laimosemion*).

*Melanorivulus* also differs from *Rivulus* by having the caudal-fin squamation not surpassing the basal portion of the fin (vs. reaching the middle of the fin), three neuromasts on the anterior supraorbital series (vs. four), absence of a black round spot with white margin on the dorsoposterior portion of caudal peduncle in females (vs. presence), dorsal hypural plate separated from ventral hypural plate by a middle gap (vs. dorsal and ventral plates fused), neural prezygapophysis of caudal vertebrae well-developed (vs. rudimentary); and, presence of teeth on the fourth ceratobranchial (vs. absence); from *Laimosemion* by having anal fin hyaline or pale pink in females (vs. intense yellow or orange); from *Cynodonichthys* by the absence of a blue blotch on the opercle (vs. presence); from *Anablepsoides* by the absence of scales on the chin (vs. presence); and, from *Atlantirivulus* by having the neuromasts of the infra-orbital series aligned around eye (vs. arranged in zigzag row) and by having a straight ventral process of the angulo-articular (vs. curved). It is also distinguished from *Cynodonichthys* and





*Anablepsoides* by the absence of the ventral process of the posttemporal.

**Included species.** *Melanorivulus apiamici* (Costa, 1989), *M. bororo* (Costa, 2007), *M. crixas* (Costa, 2007), *M. cyanopterus* (Costa, 2005), *M. dapazi* (Costa, 2005), *M. decoratus* (Costa, 1989), *M. egens* (Costa, 2005), *M. faucreticulatus* (Costa, 2007), *M. giarettai* (Costa, 2008), n. comb.); *M. illuminatus* (Costa, 2007), *M. jalapensis* (Costa, 2010), *M. javahe* (Costa, 2007), *M. karaja* (Costa, 2007), *M. kayabi* (Costa, 2007), *M. kayapo* (Costa, 2006), *M. litteratus* (Costa, 2005), *M. megaroni* (Costa, 2009), n. comb; *M. modestus* (Costa, 1991), *M. paracatuensis* (Costa, 2003), *M. parsi* (Costa, 2007), *M. parnaibensis* (Costa, 2003), *M. pictus* (Costa, 1989), *M. pinima* (Costa, 1989), *M. planaltinus* (Costa & Brasil, 2008), *M. punctatus* (Boulenger, 1895), *M. rossoi* (Costa, 2005), *M. rubromarginatus* (Costa, 2007), *M. rutilicaudus* (Costa, 2005), *M. salmonicaudus* (Costa, 2007), *M. scalaris* (Costa, 2005), *M. schuncki* (Costa & De Luca, 2011), *M. violaceus* (Costa, 1991), *M. vittatus* (Costa, 1989), *M. zygnectes* (Myers, 1927).

**Remarks.** Besides the diagnostic features listed above, *Melanorivulus* has also been diagnosed by two elements of the colour pattern: two dark grey to black oblique bars on the post-orbital region and pelvic fin with black margin in females. These derived conditions are present in all species of *Melanorivulus* except in the recently described *M. schuncki*, endemic to the eastern Brazilian Amazon (Costa & De Luca, 2011a). This species has a disjunctive geographic distribution, being the only species of the genus occurring north of the Amazonas River, possibly constituting the sister group to the assemblage comprising all other species of the genus (Costa & De Luca, 2011a). Therefore, those two colour patterns cannot be listed as diagnostic for *Melanorivulus*.

**Distribution.** Paraguay and Uruguay river basins in Bolivia, Paraguay, Brazil and Argentina; upper Paraná, Tapajós, Xingu, Araguaia, Tocantins, São Francisco, Parnaíba, and lower Amazonas river basins in central and northeastern Brazil; and isolated river basins of eastern Amazon in Amapá, northern Brazil.

**Habitat.** Species of *Melanorivulus* are only found in very shallow swampy parts of stream edges, usually less than 15 cm deep; the swamps, often

having clear water and bottom composed of orange clay, are placed in savannah areas, where streams run among rows of the buriti-palm (*Mauritia flexuosa*), an habitat known in Brazil as vereda or buritizal (Costa, 2006b, 2007a–e, 2008b, 2009b, 2010b; Costa & De Luca, 2011a). A few species occur in lowland areas (e.g., Schindler & Etzel, 2008; Costa & De Luca, 2011a) whereas the great majority is found in the plateaus of central Brazil, in altitudes varying from 200 to about 1100 m (e.g., Costa, 2007a–d; Costa & Brasil, 2008). *Melanorivulus punctatus*, considered a geographically widespread species occurring in the lowlands of south-eastern Bolivia, Paraguay, central Brazil, and north-eastern Argentina, and probably constituting a species complex, has been recorded from several kinds of habitat as described by Schindler & Etzel (2008), including swamps in the floodplains of the Paraguay River and isolated pools in the Paraguayan Chaco. In the high plateau of central Brazil, in altitudes about 750 to 1000 m, *M. faucreticulatus*, *M. litteratus*, *M. pictus*, and *M. planaltinus* occur both in veredas and in swampy shallow channels between grasslands adjacent to small rivers, the habitat known as Campo Úmido, often sympatric to cynolebiasine annual killifishes of the genus *Simpsonichthys* (e.g., Bastos & Lourenço, 1983; Costa, 2006a, 2007c; 2008e; Costa & Brasil, 2008).

### *Cynodonichthys* Meek, 1904

*Cynodonichthys* Meek, 1904: 510 (type species: *Cynodonichthys tenuis* Meek, 1904; type by original designation; gender masculine).  
*Vomerivulus* Fowler, 1944: 244 (first proposed as a subgenus; type species: *Rivulus leucurus* Fowler, 1944; type by original designation).

**Diagnosis.** *Cynodonichthys* includes medium to large-sized species, reaching between about 50 and 80 mm SL, with short fins, usually rounded, but caudal fin may be truncate in a few species. Most included species may be recognized by the presence of a yellow stripe with an upper red border on the ventral margin of the caudal fin in males. *Cynodonichthys* is distinguished from *Rivulus* by having the caudal-fin squamation not surpassing the basal portion of the fin (vs. reaching the middle of the fin), three neuromasts on the anterior supraorbital series (vs. four), absence of a blue humeral spot in males (vs. presence),



absence of a black round spot with white margin on the dorsoposterior portion of the caudal peduncle in females (vs. presence), the dorsal hypural plate separated from the ventral hypural plate by a middle gap (vs. dorsal and ventral plates fused), the neural prezygapophysis of caudal vertebrae well-developed (vs. rudimentary), and the presence of teeth on the fourth ceratobranchial (vs. absence);

*Cynodonichthys* is distinguished from *Laimosemion* by having the anal fin hyaline or pale pink in females (vs. intense yellow or orange) and by the presence of teeth on the second pharyngobranchial (vs. absence); from *Melanorivulus* by the margins of the unpaired fins not distinctively black pigmented in females (vs. black pigmentation concentrated on the whole margin of the caudal fin and on the distal margin of the dorsal and anal fins), and the presence of the dorsal part of the preopercular canal (vs. absence), of vomerine teeth (vs. absence) and of teeth on the second pharyngobranchial (vs. absence); from *Anablepsoides* by the absence of scales on the chin (vs. presence); and, from *Atlantirivulus* by having the neuromasts of the infra-orbital series aligned around eye (vs. arranged in zigzag row) and by having a straight ventral process of the angulo-articular (vs. curved). It is also distinguished from *Laimosemion*, *Melanorivulus* and *Atlantirivulus* in having a well developed ventral process on the posttemporal. In addition, *Cynodonichthys* is distinguished from *Rivulus*, *Laimosemion*, *Melanorivulus* and *Atlantirivulus* by the presence of a blue blotch on the posterior portion of the middle part of the opercle in males (vs. absence), but not clearly distinguished from *Anablepsoides* in which most species have a dark bluish grey iridescence on the opercular region, sometimes forming a distinct dark blue spot.

**Included species.** *Cynodonichthys birkhahni* (Berkenkamp & Etzel, 1992), *C. boehlkei* (Huber & Fels, 1985), *C. brunneus* (Meek & Hildebrand, 1913), *C. chucunaque* (Breder, 1925), *C. elegans* (Steindachner, 1880), *C. frommi* (Berkenkamp & Etzel, 1993), *C. fuscolineatus* (Bussing, 1980), *C. glaucus* (Bussing, 1980), *C. godmani* (Regan, 1907), *C. hendrichsi* (Alvarez & Carranza, 1952), *C. hildebrandi* (Myers, 1927), *C. isthmensis* (Garman, 1895), *C. kuelpmanni* (Berkenkamp & Etzel, 1993), *C. leucurus* (Fowler, 1944), *C. magdalenae* (Eigenmann & Henn, 1916), *C. monikae* (Berkenkamp & Etzel, 1995), *C. montium* (Hildebrand, 1938), *C. myersi*

(Hubbs, 1936), *C. pacificus* (Huber, 1992), *C. rubripunctatus* (Bussing, 1980), *C. siegfriedi* (Bussing, 1980), *C. sucubti* (Breder, 1925), *C. tenuis* Meek, 1904, *C. uroflammeus* (Bussing, 1980), *C. villwocki* (Berkenkamp & Etzel, 1997), *C. wassmanni* (Berkenkamp & Etzel, 1999), *C. weberi* (Huber, 1992).

**Distribution.** Central America and northwest South America, including Pacific and Caribbean drainages of Central America (including southern Mexico, Guatemala, Honduras, Belize, Nicaragua, Costa Rica, and Panama); river basins west of the Cordillera Occidental; and the hills between Magdalena and Maracaibo basins in Colombia (including the Magdalena and San Juan river basins).

**Habitat.** Species of *Cynodonichthys* live in streams from the sea level to altitudes about 1500 m, and are commonly found sympatric with poeciliids (e.g., Breder, 1927; Fowler, 1944; Bussing, 1980).

#### *Anablepsoides* Huber, 1992

*Anablepsoides* Huber, 1992: 43 (first proposed as a subgenus of *Rivulus* Poey; type species: *Rivulus atratus* Garman, 1895).

*Oditichthys* Huber, 1999: 49 (first proposed as a subgenus of *Rivulus* Poey; type species: *Rivulus igneus* Huber, 1991; type by original designation; gender masculine).

*Benirivulus* Costa, 2006a: 150 (first proposed as a monotypic subgenus of *Rivulus* Poey; type species: *Rivulus beniensis* Myers; type by original designation; gender masculine).

**Diagnosis.** *Anablepsoides* mostly comprises small to medium-size species, between about 30 and 60 mm SL, but it is also the only non-annual rivuline genus including large species, reaching about 100–120 mm SL. Fins are short and rounded, except the caudal fin that may be subtruncate, or elliptical and long in a few species. The great majority of included species exhibit longitudinal rows of red dots on the flank in males. *Anablepsoides* differs from all other rivuline genera by the possession of scales on the whole ventral surface of the head (vs. chin naked).

*Anablepsoides* is distinguished from *Rivulus* by having the caudal-fin squamation not surpassing the basal portion of the fin (vs. reaching the middle of the fin), three neuromasts on the anterior



supraorbital series (vs. four), absence of a blue humeral spot in males (vs. presence), absence of a black round spot with white margin on the dorsoposterior portion of the caudal peduncle in females (vs. presence), the dorsal hypural plate separated from the ventral hypural plate by a middle gap (vs. dorsal and ventral plates fused), presence of teeth on the fourth ceratobranchial (vs. absence), and the neural prezygapophysis of caudal vertebrae well-developed (vs. rudimentary); from *Laimosemion* by having the anal fin hyaline or pale pink in females (vs. intense yellow or orange) and by the presence of teeth on the second pharyngobranchial (vs. absence); from *Melanorivulus* by the margins of unpaired fins not distinctively black pigmented in females (vs. black pigmentation concentrated on the whole margin of the caudal fin and on the distal margin of the dorsal and anal fins), and the presence of the dorsal part of the preopercular canal (vs. absence), of vomerine teeth (vs. absence) and of teeth on the second pharyngobranchial (vs. absence); and, from *Atlantirivulus* by having the neuromasts of the infra-orbital series aligned around the eye (vs. arranged in zigzag row) and by having a straight ventral process of the angulo-articular (vs. curved). It is also distinguished from *Laimosemion*, *Melanorivulus* and *Atlantirivulus* in having a well developed ventral process on the posttemporal.

**Included species.** *Anablepsoides amanan* (Costa & Lazzaroto, 2008), *A. amphoreus* (Huber, 1979), *A. atratus* (Garman, 1895), *A. bahianus* (Huber, 1990), *A. beniensis* (Myers, 1927), *A. bondi* (Schultz, 1949), *A. cajariensis* (Costa & De Luca, 2011), *A. caurae* (Radda, 2004), *A. cearensis* (Costa & Vono, 2009), *A. christinae* (Huber, 1992), *A. cryptocallus* (Seegers & Huber, 1981), *A. deltaphilus* (Seegers, 1983), *A. derhami* (Fels & Huber, 1985), *A. elongatus* (Fels & de Rham, 1981), *A. erberi* (Berkenkamp, 1989), *A. gaucheri* (Keith, Nandrin & Le Bail, 2006), *A. hartii* (Boulenger, 1890), *A. holmiae* (Eigenmann, 1909), *A. igneus* (Huber, 1991), *A. immaculatus* (Thomerson, Nico & Taphorn, 1991), *A. intermittens* (Fels & de Rham, 1981), *A. iridescens* (Fels & de Rham, 1981), *A. jucundus* (Huber, 1992), *A. lanceolatus* (Eigenmann, 1909), *A. limoncochae* (Hoedeman, 1962), *A. lungi* (Berkenkamp, 1984), *A. mazaruni* (Myers, 1924), *A. micropus* (Steindachner, 1863), *A. monticola* (Staeck & Schindler, 1997), *A. ophiomimus* (Huber, 1992), *A. ornatus* (Garman, 1895), *A. peruanus* (Regan, 1903), *A. rubrolineatus* (Fels & de Rham, 1981), *A. speciosus* (Fels & de

Rham, 1981), *A. stagnatus* (Eigenmann, 1909), *A. taeniatus* (Fowler, 1945), *A. tessellatus* (Huber, 1992), *A. tocantinensis* (Costa, 2010), *A. urophthalmus* (Günther, 1866), *A. waimacui* (Eigenmann, 1909), *A. xanthonotus* (Ahl, 1926), *A. xinguensis* (Costa, 2010).

**Distribution.** Southern Lesser Antilles; Orinoco River basin in Venezuela; river basins of Guianas and adjacent parts of northeastern Venezuela and northern Brazil; Amazonas River basin in Colombia, Ecuador, Peru, Bolivia and Brazil; and small isolated river basins of northeastern Brazil.

**Habitat.** Species of *Anablepsoides* mostly inhabit shallowest parts of streams and swamps inside dense forest or in open savannah, often less than 20 cm deep (Fels & de Rham, 1982; Costa, 2006a, 2008c, 2010a; Keith et al., 2006; Costa & Lazzarotto, 2008; Costa & De Luca, 2011b). The habitat is usually located in lowlands, but a few species are recorded from mountain regions in altitudes up to 1000 m (e.g., Huber, 1979). Exceptions are *A. atratus*, *A. beniensis*, and *A. speciosus*, which are often found along shores of lakes and larger rivers (Fels & de Rham, 1982; Costa, 2006a).

#### *Atlantirivulus* Costa, 2008

*Atlantirivulus* Costa, 2008a: 46 (first proposed as a subgenus of *Rivulus* Poey; type species: *Rivulus santensis* Köhler, 1906; type by original designation; gender masculine).

**Diagnosis.** *Atlantirivulus* is a clade of small to medium-sized non-annual killifishes, reaching between 25 and 45 mm SL, always with short and rounded fins, and usually with pale colour patterns in males. *Atlantirivulus* is distinguished from all other rivulids by the neuromasts of the infra-orbital series being arranged in zigzag row (vs. aligned around eye) and by having a curved ventral process of the angulo-articular (vs. straight) (Costa, 2008a: figs. 2–3).

*Atlantirivulus* is also distinguished from *Rivulus* by having the caudal-fin squamation not surpassing the basal portion of the fin (vs. reaching the middle of the fin), three neuromasts on the anterior supraorbital series (vs. four), the absence of a blue humeral spot in males (vs. presence), absence of a black round spot with white margin on the dorsoposterior portion of caudal



peduncle in females (vs. presence), dorsal hypural plate separated from ventral hypural plate by a middle gap (vs. dorsal and ventral plates fused), presence of teeth on the fourth ceratobranchial (vs. absence), and neural prezygapophysis of caudal vertebrae well-developed (vs. rudimentary); from *Laimosemion* by having anal fin hyaline or pale pink in females (vs. intense yellow or orange) and by the presence of teeth on the second pharyngobranchial (vs. absence); from *Melanorivulus* by the margins of unpaired fins not distinctively black pigmented in females (vs. black pigmentation concentrated on the whole margin of the caudal fin and on the distal margin of the dorsal and anal fins), and the presence of the dorsal part of the preopercular canal (vs. absence), of vomerine teeth (vs. absence), and of teeth on the second pharyngobranchial (vs. absence); from *Cynodonichthys* by the absence of a blue blotch on the opercle (vs. presence); and, from *Anablepsoides* by the absence of scales on the chin (vs. presence). It is also distinguished from *Cynodonichthys* and *Anablepsoides* by the absence of the ventral process of the posttemporal.

**Included species.** *Atlantirivulus depressus* (Costa, 1991), *A. haraldsiolii* (Berkenkamp, 1984), *A. janeiroensis* (Costa, 1991), *A. jurubatibensis* (Costa, 2008), *A. lazzarotoi* (Costa, 2007), *A. luelingi* (Seegers, 1984), *A. nudiventris* (Costa & Brasil, 1991), *A. riograndensis* (Costa & Lanés, 2009), *A. santensis* (Köhler, 1906), *A. simplicis* (Costa, 2004), *A. unaensis* (Costa & De Luca, 2009).

**Distribution.** Coastal river drainages of eastern Brazil, between Una (about 10°S) and Lagoa do Peixe (about 31°S).

**Habitat.** Species of *Atlantirivulus* inhabit the shallowest parts of swamps, about 10 cm deep. Their habitat is usually inserted within dense forests, in swamps with acidic water, altitudes below 100 m (e.g., Costa, 2004d, 2007e, 2009a), but *A. jurubatibensis* is only known from open coastal swamps (Costa, 2008d). It is almost always the only fish found in the habitat.

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## Appendix 1

List of morphological characters taken from Costa (1990a, 1998a, 2004a, 2005a, 2011) and Parenti (1981), where they are described and illustrated.

### Osteology

#### Jaws, jaw suspensorium and opercular series

- [1] Autopalatine, ventral extremity, extent relative to dorsal portion of quadrate: (0) contacting; (1) not contacting.
- [2] Autopalatine, dorsal portion, prominent bony flange: (0) absent; (1) present.
- [3] Autopalatine, posterior margin, bony flange: (0) absent; (1) present.
- [4] Autopalatine, anteroventral process, anterior expansion: (0) not expanded; (1) expanded, tear-shaped.
- [5] Entopterygoid, anterior portion, extent relative to autopalatine: (0) overlapping; (1) not overlapping.
- [6] Entopterygoid, posterior portion, extent relative to metapterygoid: (0) contacting; (1) not contacting.
- [7] Metapterygoid, general shape: (0) about rectangular, dorsal and ventral portions wide, approximately equal in width; (1) about triangular, dorsal portion constricted; (2) whole bone narrowed.
- [8] Quadrate, posterior process, length relative to quadrate length without process: (0) longer; (1) equal or shorter.
- [9] Jaws, length relative to jaw suspensorium: (0) longer; (1) shorter.
- [10] Maxilla, main axis, torsion: (0) not twisted; (1) slightly twisted.
- [11] Maxilla, ventral process, anterior expansion: (0) absent; (1) present.
- [12] Maxilla, subdistal portion, anterior border, projection supporting ligament: (0) present; (1) absent.
- [13] Maxilla, distal part, abrupt widening: (0) absent; (1) present.
- [14] Maxilla, dorsal process, distal expansion: (0) absent; (1) present.
- [15] Premaxilla, subdistal portion, posterior margin, expansion: (0) present; (1) absent.
- [16] Premaxilla (in males), teeth, outer row, shape and orientation: (0) slightly curved, directed inside mouth; (1) strongly curved, directed laterally, outside mouth.
- [17] Dentary (in adult males), teeth, outer row, shape and orientation: (0) slightly curved, tip posteriorly directed; (1) strongly curved, tip posterolaterally directed; (2) slightly curved, tip anteriorly directed.
- [18] Dentary (in adult males), teeth, outer row, size related to adjacent teeth of inner rows: (0) two or three times bigger; (1) about five times bigger.
- [19] Dentary, coronoid process, shape: (0) robust; (1) slender.
- [20] Dentary, posteroventral process, shape: (0) pointed, narrow; (1) truncate, broad.
- [21] Angulo-articular, ventral process, shape: (0) wide, about rectangular; (1) narrow, about triangular.
- [22] Angulo-articular, ventral process, development: (0) well-developed; (1) rudimentary.
- [23] Angulo-articular, ventral process, axis orientation: (0) straight; (1) curved.
- [24] Angulo-articular, ventral process, direction and extent relative to dentary: (0) anteroventrally directed, not reaching dentary; (1) anteriorly directed, often terminating in long sharp point, surpassing or in close proximity to vertical through posterior limit of dentary.
- [25] Symplectic, dorsal margin, expansion towards entopterygoid: (0) absent; (1) present; (?) rudimentary expansion, often absent.
- [26] Hyomandibula, area adjacent to metapterygoid, foramen: (0) absent; (1) present.
- [27] Preopercle, shape: (0) robust, L-shaped, with a well developed anteromedian rim; (1) thin, C-shaped, with a reduced anteromedian rim.
- [28] Preopercle, dorsal arm, shape: (0) blunt; (1) pointed.
- [29] Preopercle, dorsal arm, length relative to anteroventral arm: (0) approximately equal or shorter; (1) distinctively longer.
- [30] Opercle, ventro-posterior part, expansion: (0) absent; (1) present. Remarks: all taxa exhibiting the apomorphic condition also have the dorsal portion of the opercle distinctively longer than the ventral portion (vs. about equal in length in the remaining taxa), thus considered as a dependent condition.



### Hyoid and branchial arches

- [31] Interhyal, ossification: (0) ossified; (1) cartilaginous.
- [32] Interhyal, development: (0) well-developed; (1) rudimentary or absent.
- [33] Basihyal, length relative to longitudinal length of three basibranchials: (0) shorter; (1) longer.
- [34] Basihyal, cartilaginous portion, length relative to total basihyal length: (0) about half; (1) about one third; (2) about one tenth.
- [35] Urohyal, dorsal process, development: (0) minute; (1) well-developed.
- [36] Urohyal, anterior process, expansion: (0) absent; (1) present.
- [37] First epibranchial, width of proximal tip relative to distal tip: (0) about 5–6 times; (1) about 1–3 times.
- [38] First epibranchial, flexion: (0) unbowed; (1) bowed.
- [39] First epibranchial, torsion: (0) untwisted; (1) twisted.
- [40] Second epibranchial, subdistal process: (0) present; (1) absent.
- [41] Third epibranchial, uncinat process, angle formed with distal process: (0) about 90°; (1) about 45–60°.
- [42] Third epibranchial, uncinat process, development: (0) well-developed; (1) rudimentary.
- [43] Second pharyngobranchial, distal border, notch close to condyle: (0) absent; (1) present.
- [44] Second pharyngobranchial, medial border, expansion: (0) not expanded; (1) expanded.
- [45] Second pharyngobranchial, medial flap: (0) absent; (1) present.
- [46] Second pharyngobranchial, teeth: (0) present; (1) absent; (?) present or absent.
- [47] First hypobranchial, medial edge: (0) unbranched or with slight division; (1) deeply branched.
- [48] First hypobranchial, lateral edge, articular facet extension relative to apical cartilage of first ceratobranchial: (0) restricted to articulation area: (1) extended.
- [49] Second hypobranchial, medial edge: (0) unbranched or with slight division; (1) deeply branched.
- [50] Fourth ceratobranchial, ventral process, orientation: (0) ventral; (1) posterior.

### Neurocranium

- [51] Lateral ethmoid, medial extent expressed by cartilaginous space width between medial margin of bone and vomer and parasphenoid relative to anterior parasphenoid width: (0) wider; (1) narrower.
- [52] Lateral ethmoid, anterior retrorse process: (0) rudimentary; (1) well-developed.
- [53] Lateral ethmoid, anterior retrorse process, extent relative to lateral ethmoid: (0) not reaching; (1) contacting, often fused.
- [54] Parasphenoid, anterolateral process, extent relative to pterosphenoid: (0) short, not reaching; (1) long, touching or attached to.

- [55] Frontal, lateral border, shape: (0) approximately straight; (1) concave.
- [56] Lachrymal, ventral portion, expansion: (0) absent; (1) present.
- [57] Dermosphenotic, development: (0) well developed; (1) minute.
- [58] Vomerine teeth: (0) present; (1) absent.

### Vertebrae and unpaired fin skeleton

- [59] First vertebra, latero-dorsal laminar process: (0) present; (1) absent.
- [60] First vertebra, anteriorly directed paired process: (0) absent; (1) present.
- [61] Hypurals, middle gap: (0) present; (1) absent; (?) plates often partly or completely fused, gap rudimentary.
- [62] Anal fin, anterior proximal radials, anterior and posterior margin extent: (0) not extended, margins almost straight; (1) extended, margins convex, consequently reducing space between radials.
- [63] Anal fin, first two proximal radials, fusion: (0) not fused; (1) fused.

### Shoulder and pelvic girdle

- [64] Posttemporal, ventral process: (0) present; (1) absent.
- [65] Posttemporal, prominent lateral keel: (0) absent; (1) present.
- [66] First postcleithrum: (0) present; (1) absent.
- [67] Cleithrum, posterior flange: (0) present; (1) absent.
- [68] Fourth pectoral radial, ventral expansion: (0) absent; (1) present.
- [69] Pelvic bone, thickness and processes, development: (0) thick, processes well-developed; (1) thin, ischial and lateral processes rudimentary or absent.
- [70] Pelvic bones, relative medial position: (0) separated by interspace; (1) overlapped.

### External morphology

#### Head

- [71] Membrane between preopercular laterosensory series and isthmus, middle gap: (0) present; (1) absent.
- [72] Ventral squamation, anterior extent: (0) reaching corner of pre-opercular series; (1) reaching anterior end of pre-opercular series; (2) reaching chin.
- [73] Frontal scales, geometric arrangement: (0) transverse; (1) circular.
- [74] Frontal scales, symmetry: (0) present; (1) absent.
- [75] Frontal squamation, modal arrangement-pattern: (0) G; (1) E; (2) D; (3) F.
- [76] E-scales, relative position: (0) overlapped; (1) not overlapped.

#### Trunk

- [77] Flank in males, contact organs: (0) absent; (1) present.



[78] Venter in females, urogenital papilla, shape: (0) minute protuberance around urogenital opening; (1) prominent pocket-like structure around urogenital opening, often overlapping anal-fin origin.

#### Fins

- [79] Pectoral fin in males, contact organs: (0) absent; (1) present.
- [80] Pectoral fin in males, posterior extremity, shape: (0) rounded; (1) pointed.
- [81] Pelvic fin in males, tip, filamentous rays: (0) absent; (1) present.
- [82] Pelvic fins, medial fusion: (0) separated; (1) united.
- [83] Pelvic fin, number: (0) five or six; (1) seven; (2) eight; (3) nine.
- [84] Anal fin, basal portion, scales: (0) absent; (1) present.
- [85] Anal fin in females, distal length relative to fin base: (0) shorter; (1) longer.
- [86] Anal fin in females, thickness relative to male anal fin: (0) equal; (1) distinctively thicker.
- [87] Caudal fin in males, posterior margin, filaments forming fringed border: (0) absent; (1) present.
- [88] Caudal fin in males, length relative to standard length: (0) clearly less than half; (1) about half or longer.
- [89] Caudal fin in older males, squamation, mid-horizontal extent: (0) restricted to basal portion of fin; (1) approximately reaching middle of fin.

#### Laterosensory system

- [90] Supra-orbital series, anterior section, neuromast, number: (0) three; (1) four; (2) six or seven.
- [91] Supra-orbital series, posterior section, arrangement and number of neuromasts: (0) arranged triangularly, containing 3 neuromasts; (1) arranged semi-circularly, containing 4–6 neuromasts; (2) arranged along a curved line, containing 7–8 neuromasts.
- [92] Infra-orbital series, neuromasts, arrangement: (0) aligned; (1) on zigzag row.
- [93] Preorbital series, arrangement and number of neuromasts: (0) restricted to zone close to orbit, containing 1–3 neuromasts; (1) extending towards supraorbital neuromast series, containing 4–6 neuromasts; (2) contacting supraorbital neuromast series, containing 8 neuromasts.
- [94] Preopercular series, upper section, canal: (0) close; (1) open.
- [95] Preopercular series, relative position of upper and lower sections: (0) separated by interspace; (1) continuous.
- [96] Mandibular series, number of neuromasts: (0) four anterior neuromasts separated by interspace from one or two posterior neuromasts; (1) 7–11 neuromasts continuously arranged; (2) 17–18 continu-

ously arranged; (3) three anterior neuromasts separated by interspace from one posterior neuromast; (–) inapplicable due to mandibular and preopercular series being continuous.

#### Male colour patterns

- [97] Flank, humeral region, large iridescent blue blotch: (0) absent; (1) present.
- [98] Flank, humeral region, small orange spots: (0) absent; (1) present.
- [99] Head, iris, dark grey to black bar through centre of eye: (0) absent; (1) present.
- [100] Head, anterior suborbital region, distinctive dark grey to black bar: (0) absent; (1) present.
- [101] Head, opercular region, regular reticulate pattern formed by iridescent colour on middle of scales contrasting with dark orangish brown pigment along entire scale margins: (0) absent; (1) present.
- [102] Head, lower jaw, colour: (0) not distinctively coloured; (1) dark grey to black.
- [103] Head, middle opercular region, blue blotch: (0) absent; (1) present.
- [104] Head, opercular region, dark bluish grey iridescence: (0) absent; (1) present.
- [105] Dorsal fin, distal region, red line on fin rays: (0) absent; (1) present.
- [106] Anal fin, basal region, dark grey to black ground colour with row of white to yellow spots: (0) absent; (1) present.
- [107] Caudal fin, ventral portion, diffuse red stripe: (0) absent; (1) present.
- [108] Caudal fin, ventral portion, dark orange stripe with narrow light yellow and dark reddish brown upper margin: (0) absent; (1) present.
- [109] Caudal fin, ventral portion, light yellow stripe with broad dark red upper margin: (0) absent; (1) present.
- [110] Caudal fin, middle portion, red bars: (0) absent; (1) present.
- [111] Pectoral fin, dark grey to black marks vertically crossing all fin extension: (0) absent; (1) present.

#### Female colour patterns

- [112] Flank, dark brown stripes: (0) absent; (1) present.
- [113] Caudal peduncle, posterodorsal end, round black spot with white margin: (0) absent; (1) present.
- [114] Caudal fin, base, dorsal portion, rounded black spot with white dot on anterior margin: (0) absent; (1) present.
- [115] Anal fin, colour: (0) hyaline; (1) bright yellow or orange.
- [116] Unpaired fins, margins, black zone: (0) absent; (1) present.

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