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Relationships and taxonomy of the killifish genus *Rivulus* (Cyprinodontiformes: Aplocheiloidei: Rivulidae) from the Brazilian Amazonas river basin, with notes on historical ecology

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Abstract

Relationships among species of *Rivulus* endemic to the Brazilian Amazonas river basin are evaluated through an analysis of morphological characters, including terminal taxa representative of all *Rivulus* lineages. Based on the present morphological phylogeny and previous molecular analyses, seven subgenera are recognized: *Rivulus*, *Cynodonichthys*, *Anablepsoides*, *Benirivulus* n. subgen., *Laimosemion*, *Owiye* n. subgen., and *Melanorivulus* n. subgen. *Benirivulus* is diagnosed by a unique colour pattern and includes a single species, *R. beniensis*, from the rio Madeira drainage; *Owiye* is diagnosed by the absence of dermosphenotic, a derived pattern of frontal squamation, and a colour pattern of the mandibular region, and includes species from the Amazonas and Orinoco river basins; *Melanorivulus* is diagnosed by an apomorphic morphology of preopercle, and derived colour patterns of male postorbital region and female unpaired fins, and includes species from southern Amazonian tributaries, Paraná-Paraguay river system, and Parnaíba and São Francisco river basins. Eighteen species from the Amazonas river basin of Brazil are recognized as valid: *R. urophthalmus*, *R. taeniatus*, *R. micropus*, *R. ornatus*, *R. beniensis*, *R. strigatus*, and *R. dibaphus*, which are herein redescribed, and *R. atratus*, *R. romeri*, *R. kirovskyi*, *R. uatuman*, *R. uakti*, *R. amanapira*, *R. tecminae*, *R. modestus*, *R. zygonectes*, *R. violaceus*, and *R. litteratus*, described or redescribed recently. Field data indicate that species of different lineages included in the clade comprising *Benirivulus*, *Laimosemion*, *Owiye*, and *Melanorivulus* are found in different kinds of aquatic environments, suggesting a divergent evolution for habitat preference.

Resumo

As relações de parentesco entre espécies de *Rivulus* endêmicas da bacia amazônica brasileira são avaliadas através de uma análise de caracteres morfológicos, incluindo táxons terminais representativos de todas as linhagens de *Rivulus*. Com base na presente filogenia morfológica e em análises moleculares anteriores, sete subgêneros são reconhecidos: *Rivulus*, *Cynodonichthys*, *Anablepsoides*, *Benirivulus* n. subgen., *Laimosemion*, *Owiye* n. subgen., e *Melanorivulus* n. subgen. *Benirivulus* é diagnosticado por um padrão de colorido exclusivo e inclui uma única espécie, *R. beniensis*, da drenagem do rio Madeira; *Owiye* é diagnosticado pela ausência de dermosfenótico, um padrão de escamação frontal derivado e um padrão de colorido da região mandibular, e inclui espécies das bacias dos rios Amazonas e Orinoco; *Melanorivulus* é diagnosticado pela morfologia apomórfica do pré-opérculo e pelos padrões de colorido derivados de região pós-orbital de macho e de nadadeiras ímpares de fêmeas, e inclui espécies dos tributários amazôni-

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Zusammenfassung

As relações de parentesco entre espécies de *Rivulus* endêmicas da bacia amazônica brasileira são avaliadas através de uma análise de caracteres morfológicos, incluindo táxons terminais representativos de todas as linhagens de *Rivulus*. Com base na presente filogenia morfológica e em análises moleculares anteriores, sete subgêneros são reconhecidos: *Rivulus*, *Cynodonichthys*, *Anablepsoides*, *Benirivulus* n. subgen., *Laimosemion*, *Owiye* n. subgen., e *Melanorivulus* n. subgen. *Benirivulus* é diagnosticado por um padrão de colorido exclusivo e inclui uma única espécie, *R. beniensis*, da drenagem do rio Madeira; *Owiye* é diagnosticado pela ausência de dermosfenótico, um padrão de escamação frontal derivado e um padrão de colorido da região mandibular, e inclui espécies das bacias dos rios Amazonas e Orinoco; *Melanorivulus* é diagnosticado pela morfologia apomórfica do pré-opérculo e pelos padrões de colorido derivados de região pós-orbital de macho e de nadadeiras ímpares de fêmeas, e inclui espécies dos tributários amazôni-

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Résumé

Des affinités entre des espèces de *Rivulus* endémiques du bassin brésilien de l'Amazonie sont évaluées au moyen d'une analyse de caractéristiques morphologiques, incluant des taxons terminaux représentatifs de tous les lignages de *Rivulus*. Sur base de la phylogénie morphologique actuelle et d'analyses moléculaires antérieures, sept sous-genres sont identifiés: *Rivulus*, *Cynodonichthys*, *Anablepsoides*, *Benirivulus* n. subgen., *Laimosemion*, *Owiyeye* n. subgen. et *Melanorivulus* n. subgen. *Benirivulus* se distingue par un patron de coloration unique et comprend une seule espèce, *R. beniensis*, du système du Rio Madeira; *Owiyeye* est distinct par l'absence de dermosphénotique, un patron dérivé d'écaillés frontales, et un patron de coloration de la région mandibulaire, et inclut des espèces des bassins de l'Amazonie et de l'Orénoque; *Melanorivulus* se distingue par une morphologie apomorphique du préopercule, des patrons de colorations dérivés de la région postorbitale du mâle et des nageoires impaires de la femelle et compte des espèces des tributaires sud de l'Amazonie, du système du Paraná-Paraguay, du bassin du Paranaíba et du São Francisco. Dix-huit espèces du bassin brésilien de l'Amazonie sont reconnues: *R. urophthalmus*, *R. taeniatus*, *R. micropus*, *R. ornatus*, *R. beniensis*, *R. strigatus* et *R. dibaphus*, qui sont redécrits ici, et *R. atratus*, *R. romeri*, *R. kirovskyi*, *R. uatuman*, *R. uakti*, *R. amanapira*, *R. tecminae*, *R. modestus*, *R. zygonectes*, *R. violaceus* et *R. litteratus*, décrits ou redécrits récemment. Des données de terrain révèlent que des espèces de différents lignages faisant partie du clade comprenant *Benirivulus*, *Laimosemion*, *Owiyeye* et *Melanorivulus* se trouvent dans diverses sortes d'environnements aquatiques, suggérant une évolution divergente en matière de choix d'habitat.

Sommario

As relações de parentesco entre espécies de *Rivulus* endêmicas da bacia amazônica brasileira são avaliadas através de uma análise de caracteres morfológicos, incluindo taxons terminais representativos de todas as linhagens de *Rivulus*. Com base na presente filogenia morfológica e em análises moleculares anteriores, sete subgêneros são reconhecidos: *Rivulus*, *Cynodonichthys*, *Anablepsoides*, *Benirivulus* n. subgen., *Laimosemion*, *Owiyeye* n. subgen., e *Melanorivulus* n.

subgen. *Benirivulus* é diagnosticado por um padrão de colorido exclusivo e inclui uma única espécie, *R. beniensis*, da drenagem do rio Madeira; *Owiyeye* é diagnosticado pela ausência de dermosfenótico, um padrão de escamação frontal derivado e um padrão de colorido da região mandibular, e inclui espécies das bacias dos rios Amazonas e Orinoco; *Melanorivulus* é diagnosticado pela morfologia apomórfica do pré-opérculo e pelos padrões de colorido derivados de região pós-orbital de macho e de nadadeiras ímpares de fêmeas, e inclui espécies dos tributários amazônicos meridionais, do sistema de rios Paraná-Paraguai, e bacias dos rios Paranaíba e São Francisco. Dezoito espécies da bacia do rio Amazonas do Brasil são reconhecidas como válidas: *R. urophthalmus*, *R. taeniatus*, *R. micropus*, *R. ornatus*, *R. beniensis*, *R. strigatus* e *R. dibaphus*, que são aqui redescritas, e *R. atratus*, *R. romeri*, *R. kirovskyi*, *R. uatuman*, *R. uakti*, *R. amanapira*, *R. tecminae*, *R. modestus*, *R. zygonectes*, *R. violaceus* e *R. litteratus*, recentemente descritas ou redescritas. Dados de campo indicam que espécies de distintas linhagens, incluídas no clado que compreende *Benirivulus*, *Laimosemion*, *Owiyeye* e *Melanorivulus*, são encontradas em tipos deferentes de ambientes aquáticos, sugerindo uma evolução divergente para preferência de habitats.

Introduction

Rivulus Poey, 1860 is the most geographically widespread and diversified genus of Neotropical aplocheiloid killifishes (e.g., Costa 2003a). It is also the most taxonomically problematic genus of Neotropical aplocheiloids, in spite of recent efforts to clarify the taxonomic status of included species, among which many are still poorly defined. Taxonomic problems are due to: great number of included species (over 100 nominal species) in a wide geographic range (from Mexico, about 20° N, to Argentina, about 30° S, including Caribbean islands), making it difficult to develop taxonomic studies encompassing comparative material from all regions; brief descriptions, often including only a few characters insufficient to diagnose taxa; bad preservation of type specimens; equivocal synonymies (e.g., Garman 1895); and, unknown data on colour patterns of live specimens in older descriptions.

Rivulus was erected to include a single species from Cuba, *R. cylindraceus* Poey, 1860 (Poey 1860). Since then, over 120 nominal species were incorporated into *Rivulus*, some subgenera were described, and some species groups were diagnosed (e.g. Hoedeman 1959; Huber 1992; Costa 1995a, 2003a). Some studies have been directed to the taxonomy of *Rivulus* in some regularly and recently explored zoogeographical areas, including: Central America (e.g., Bussing 1980; Etzel & Berkenkamp 1992;

Berkenkamp & Etzel 1992, 1993a, 1993b, 1995, 1997, 1999), Guianas (Hoedeman 1959; Huber 1979, 1991; Vermeulen & Isbrücker 2000), río Orinoco basin (Thomerson *et al.* 1991a, 1991b, 1992; Lasso *et al.* 1992; Thomerson & Taphorn 1992, 1993), Peruvian Amazon (e.g., Fels & Huber 1985; Fels & de Rham 1982), and central and south-eastern Brazil (e.g., Seegers 1984; Costa 1989, 1991, 1995a, 2003c, 2004g, 2005a; Costa & Brasil 1991). However, species of *Rivulus* endemic to the Brazilian Amazon have received little attention, except for recent descriptions of new species from the rio Negro drainage and near localities (e.g. Costa 2003b, 2004c, 2004d, 2004e). Among species of *Rivulus* from the Brazilian Amazon are some of the oldest species names presently assigned to the genus, therefore making them important keys in solving taxonomic problems.

The only genus today considered to be a synonym of *Rivulus* is *Cynodonichthys* Meek, 1904, which was described to include *C. tenuis* Meek from Mexico (Meek 1904). *Cynodonichthys* has been placed in the synonymy of *Rivulus* since Regan (1907). *Vomerivulus* Fowler, 1944 was proposed as a new monotypic subgenus of *Rivulus* based on the possession of vomerine teeth in its type species, *R. leucurus* Fowler, 1944, from the río Juradó, Colombia (Fowler 1944). However, possession of vomerine teeth is a plesiomorphic condition in rivulids, occurring in most aplocheiloids, including *R. cylindraceus*, the type species of *Rivulus* (e.g. Costa 1998a, 1998b).

Hoedeman (1959, 1961), based on combinations of morphological features such as presence of caudal spot, details of colour patterns, maximum adult size, frontal squamation pattern, and number of longitudinal scales, divided *Rivulus* into species groups. Huber (1992) adopted this classification, recognizing a total of 18 assemblages (i.e., superspecies), besides describing a new monotypic subgenus, *Anablepsoides* Huber, 1992, for *R. atratus* Garman, 1895. Subsequently, two Huber's superspecies were formally recognized as new subgenera, *Oditichthys* Huber, 1999 and *Laimosemion* Huber, 1999 (Huber 1999). Some species groups have been consistently supported both by osteological (Costa 1998a) and molecular data (Murphy & Collier 1996, Murphy *et al.* 1999, Hrbek & Larson 1999, Hrbek *et al.* 2004).

Since the first taxonomic revision of the species grouped into the cyprinodontiform assemblage today known as the Rivulidae by Garman (1895), until recent years (Parenti 1981), *Rivulus* was defined by a combination of plesiomorphic mor-

phological features. In other words, *Rivulus* was diagnosed by the absence of the distinctive features (i.e., apomorphies) that diagnose the other rivulid genera (e.g. long fins in *Pterolebias* Garman, 1895, *vs.* short fins in *Rivulus*; numerous dorsal- and anal-fin rays in *Cynolebias* Steindachner, 1876, *vs.* few rays in *Rivulus*) (Garman 1895, Regan 1912, Myers 1927). In addition, *Rivulus* contained species living in perennial aquatic biotopes, whereas the remaining rivulids comprised species inhabiting seasonal pools.

Weitzman & Wourms (1967) suggested that rivulids were derived from a *Rivulus*-like ancestor. Parenti (1981), based on morphological characters, provided the first phylogenetic analysis of rivulids, in which *Rivulus* was considered a paraphyletic group with their nominal species included at least in two basal rivulid lineages. Among the five nominal species of *Rivulus* examined in Parenti's analysis, *R. stellifer* Thomerson & Turner, 1973 (transferred to *Rachovia* Myers by Costa 1998a) and *R. hartii* (Boulenger, 1890) were placed in an assemblage termed "*Rivulus*", that would be more closely related to all other rivulid genera (e.g. *Cynolebias*; *Pterolebias*; *Trigonectes* Myers, 1925) than to *Rivulus*, which would include the type species *R. cylindraceus*, and *R. marmoratus* Poey, 1880 (transferred to *Kryptolebias* Costa, 2004 by Costa 2004a) and *R. tenuis* (Meek, 1904), among the species analysed in this study. Consequently, *Rivulus* was considered to be the sister group to a clade including "*Rivulus*" and all other rivulids, which was diagnosed by an apomorphic cartilaginous interhyal (*vs.* ossified in *Rivulus*) and a derived number of pelvic-fin rays (seven in "*Rivulus*" and the remaining rivulids, *vs.* six in *Rivulus*). However, Parenti (1981) did not find synapomorphies corroborating the monophyly of *Rivulus* or of "*Rivulus*".

Costa (1990), in a phylogenetic analysis based on morphological and behavioural traits, confirmed the presence of an ossified interhyal in some species then placed in *Rivulus*, but demonstrated that the number of seven pelvic-fin rays is not informative to define a rivulid clade. *Rivulus* was considered to be a monophyletic group based on the morphology of the shoulder girdle and the neural prezygapophyses of caudal vertebrae. A similar general phylogenetic hypothesis among rivulid lineages was obtained by Murphy & Collier (1997) using mitochondrial genes of seven rivulid species, but monophyly of *Rivulus* was not properly tested since only two species of *Rivulus* were included in the analysis.

Costa (1998a), in a subsequent phylogenetic study of rivulids, including new taxa and re-evaluating previously described morphological and behavioural characters, noted that, in fact, *R. cylindraceus*, the type species of *Rivulus*, not available in the previous study, has a cartilaginous interhyal. Among the new characters analysed, Costa (1998a) found that species of *Rivulus* with an ossified interhyal, i.e. *R. brasiliensis* (Valenciennes, 1821), *R. caudomarginatus* Seegers, 1984, and *R. ocellatus* Hensel, 1868, all later transferred to *Kryptolebias* by Costa (2004a) also exhibit other putative plesiomorphic conditions, and thus monophyly of *Rivulus* was weakly supported. Subsequent molecular analyses (Murphy *et al.* 1999, Hrbek & Larson 1999, Hrbek *et al.* 2004) indicated *Rivulus* as a paraphyletic group, with different assemblages as successive sister groups to a clade including annual fish genera.

Costa (2004a) described *Kryptolebias* to include species previously placed in *Rivulus* with an osseous interhyal, among other morphological features. *Kryptolebias* was considered to be the sister group to a clade including *Rivulus* and all other rivulids (Costa 2004a, 2004b, 2004c), a hypothesis supported by molecular data (Vermeulen & Hrbek 2005).

Since the description of *Kryptolebias* and the consequent transference of some species of *Rivulus* to *Kryptolebias*, a re-evaluation of the generic placement of species maintained in *Rivulus* became necessary, as well as a reassessment of morphological characters employed to define subgroups of *Rivulus*. The objectives of the present study are: to test hypotheses of relationships among species of *Rivulus* from the Brazilian Amazon to other rivulids, based on morphological characters discussed and illustrated in previous studies (e.g., Costa 1990, 1998, 2004, 2005b); to diagnose and to update data on the taxonomy and distribution of species of *Rivulus* from the Brazilian Amazonas basin, providing redescriptions of poorly known species; to re-evaluate morphological diagnoses for nominal subgenera and to propose a new classification in order to formally accommodate hypotheses derived from recent phylogenetic studies.

Material and methods

Material pertinent to the taxonomic study on *Rivulus* from the Brazilian Amazonas river basin is listed in the taxonomical accounts below. Data on material is given in the following order: catalogue number, number of specimens; country: major

political division: locality; collectors, and date of collection. Acronyms for institutions are: ANSP, Academy of Natural Sciences, Philadelphia; BMNH, The Natural History Museum, London; CAS, California Academy of Sciences, San Francisco; CBF, Colección Boliviana de Fauna, Museo Nacional de Historia Natural, La Paz; FMNH, Field Museum of Natural History, Chicago; INPA, Instituto Nacional de Pesquisas da Amazônia, Manaus; MCNG, Museo de Ciencias Naturales de la Universidad Nacional Experimental de los Llanos Occidentales, Guanare; MCP, Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre; MCZ, Museum of Comparative Zoology, Cambridge; MHNC, Museo Nacional de Historia Natural, La Havana; MNRJ, Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro; MZUSP, Museu de Zoologia, Universidade de São Paulo, São Paulo; NMW, Naturhistorisches Museum Wien, Vienna; UFPB, Universidade Federal da Paraíba, João Pessoa; UFRJ, Instituto de Biologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro; UMMZ, University of Michigan, Museum of Zoology, Ann Arbor; UNT, Universidade Federal do Tocantins, Porto Nacional; USNM, National Museum of Natural History (former United States National Museum), Smithsonian Institution, Washington; ZFMK, Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn; and, ZUEC, Departamento de Zoologia da Universidade Estadual de Campinas, Campinas. Geographic entities are presented by their regional names (e.g., rio or río, igarapé, lago), which are not capitalized following Portuguese and Spanish grammars; this practice is important to avoid English style and generalizations when translating South American localities, which become data inaccurate and may incur errors (see also Menezes & Weitzman 1990, and Reis 1997 for further justification for this widely employed practice). EPA, that appears as collectors of some material, means Expedição Permanente da Amazônia, a cooperative project between MZUSP, INPA and Museu Paraense Emílio Goeldi, Belém; NEAMB means Núcleo de Estudos Ambientais da Universidade Federal do Tocantins. The remaining material of Aplocheiloidei taxa examined in the present study is listed in the Appendix 1.

Measurements and counts follow Costa (1995b). Measurements are presented as percentages of standard length (SL), except for those related to head morphology, expressed as percentages of head length. Fin-ray counts include all elements. Number

of vertebrae, gill rakers, and caudal-fin rays were recorded only from cleared and stained specimens. The compound caudal centrum was counted as a single element. Osteological preparations were made according to Taylor & Van Dyke (1985). Terminology for frontal squamation (i.e. A-H) follows Hoedeman (1958); determination of frontal squamation patterns (i.e. D, E, F) is according to Hoedeman (1958) (i.e. frontal scale with all margins free), except S-pattern (i.e. a scale just posterior to snout with all margins free) which is according to Huber (1992). Terminology for cephalic neuromast series follows Costa (2001).

The phylogenetic analysis is according to the cladistic methodology applied to morphological characters (e.g. Kitching *et al.* 1998, Wiens 2000). Terminal taxa were species of *Rivulus* occurring in the Brazilian Amazonas basin, species of *Rivulus* representing all main lineages from all zoogeographic regions inserted in the geographic area of the genus, and species of rivulid genera representing lineages closely related to *Rivulus* according to recent phylogenetic studies (Costa 1998a, Murphy *et al.* 1999, Hrbek & Larson 1999): *Aphyolebias boticarioi* Costa, 2004, *Gnatholebias hoignei* (Thomerson, 1974), *Micromoema xiphophora* (Thomerson & Taphorn, 1992), *Moema apurinan* Costa, 2004, *Neofundulus paraguayensis* (Eigenmann & Kennedy, 1903), *Pituna compacta* (Myers, 1927), *Rachovia maculipinnis* (Radda, 1964), *Rachovia stellifer*, *Renova oscari* Thomerson & Taphorn, 1995, and *Trigonectes rubromarginatus* Costa, 1990. Four levels of outgroups were included: *Prorivulus auriferus* Costa, Lima & Suzart, 2004, and *Kryptolebias brasiliensis*, representing the successive most basal lineages of the Rivulidae (Costa 2004a, 2004c); *Scriptaphyosemion guignardi* (Romand, 1981) of the Nothobranchidae, the sister group of Rivulidae (Murphy & Collier 1997, Costa 2004a); and, *Aplocheilus panchax* (Hamilton-Buchanan, 1822) of the Aplocheilidae, the sister group of Nothobranchidae plus Rivulidae (Murphy & Collier 1997, Costa 2004a).

Characters were obtained from previous phylogenetic studies (e.g. Parenti 1981; Costa 1990, 1998a, 2005b). Character states of multi-state characters were treated as ordered whenever possible. Boundaries between states of quantitative characters were taken from Costa (2005b), which were determined to accommodate the best estimate of range observed for each terminal species included in that category (i.e. character state). All characters and character

states used in the phylogenetic analysis are listed and coded in the Appendix 2 and are organized in the data matrix of Appendix 3. Most parsimonious cladograms, consistency indices (CI) and retention indices (RI) were obtained using the algorithm *mhennig**; *bb** of the program Hennig86 (Farris 1988). TreeGardener 2.2.1 (Ramos 1996) was used for optimisation of character state changes in the strict consensus tree of most parsimonious cladograms, using ACCTRAN. Bootstrap analysis (Felsenstein 1985) was used to establish nodal support through the simple heuristic algorithm of PAUP 4.0 (Swofford 1998) with 1000 replicates.

Results

Phylogenetic analysis

The phylogenetic analysis is based on a re-examination of previously reported, discussed and illustrated morphological characters (e.g. Parenti 1981; Costa 1990, 1998a, 2005b), which are listed in the Appendix 2. Their distribution among taxa examined appears in the data matrix (Appendix 3).

Six most parsimonious cladograms were found (tree length = 364, CI = 0.42, RI = 0.72). They differ only in the position of *R. igneus*, (i.e., as sister to *R. hartii* or to *R. amphoreus* Huber, 1979), and *R. uatuman* Costa, 2004 (i.e., as sister to *R. romeri* Costa, 2003 or to *R. kirovskyi* Costa, 2004). The strict consensus tree (tree length = 367, CI = 0.41, RI = 0.71) is illustrated in Fig. 1.

Taxonomic accounts

Rivulus is here formally divided into seven subgenera, which are supported both by morphological (the present analysis) and molecular data (e.g. Murphy *et al.* 1999, Hrbek & Larson 1999; see discussion below). Subgenera of *Rivulus* and species occurring in the Brazilian Amazonas basin are listed and diagnosed below. Diagnoses of subgenera are synapomorphies obtained from the above phylogenetic analysis; numbers in parentheses refer to characters states listed in Appendix 2.

Rivulus Poey, 1860

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

Subgenus *Rivulus* Poey, 1860

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

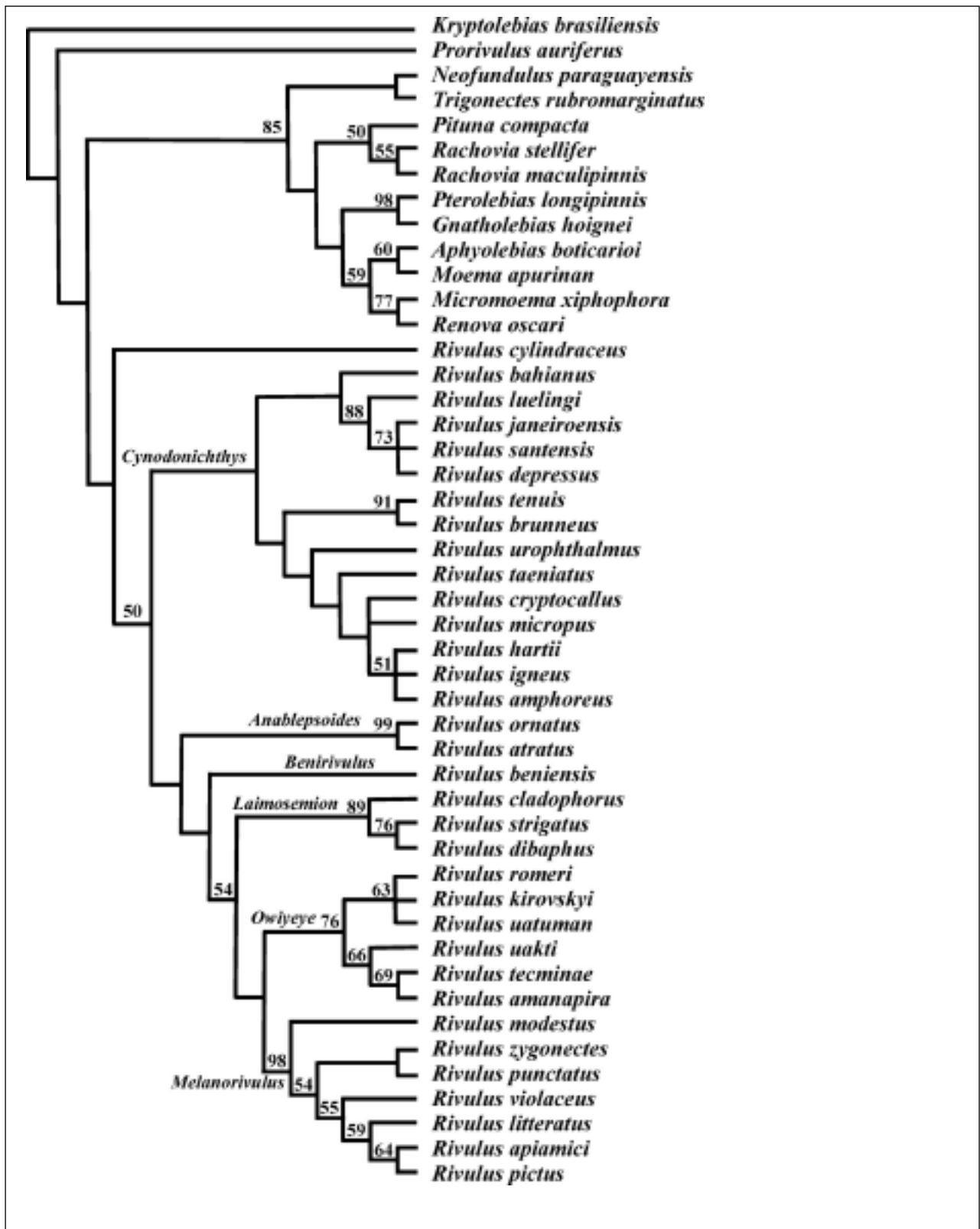


Fig. 1. Strict consensus of six equally parsimonious shortest phylogenies among 47 species of the Rivulidae (L = 367, CI = 0.41, RI = 0.71). Numbers above branches are bootstrap values.

Diagnosis

Distinguished from all other congeners by the possession of the following apomorphic features: hypurals completely fused to form a single plate (45.3), about 60% of the anterior portion of the caudal fin covered by scales (82.2), four neuromasts on the anterior supraorbital series (85.1), and a dark metallic blue humeral blotch in male.

Included species

R. cylindraceus Poey, 1860, *R. insulaepinorum* De La Cruz & Dubitsky, 1976 and *R. roloffi* Roloff, 1938.

Distribution

Rivers basins of Cuba and Republica Dominicana.

Subgenus *Cynodonichthys* Meek, 1904

Cynodonichthys Meek, 1904: 98 (type species: *Cynodonichthys tenuis* Meek; type by original designation).

Vomerivulus Fowler, 1944: 244 (type species: *Rivulus leucurus* Fowler; type by original designation).

Oditichthys Huber, 1999: 49 (type species: *Rivulus igneus* Huber; type by original designation).

Diagnosis

Tentatively diagnosed by the presence of yellow stripes on dorsal and ventral margins of caudal fin in male (101.1, 102.1), a condition inconspicuous or absent in some members of *Cynodonichthys* (i.e. reversals), but also exhibited by some species of *Owiyeye* (i.e. homoplasies).

Included species: *Rivulus amphoreus* Huber, 1979, *R. bahianus* Huber, 1990, *R. birkhahni* Berkenkamp & Etzel, 1992, *R. boehlkei* Huber & Fels, 1985, *R. brunneus* Meek & Hildebrand, 1913, *R. christinae* Huber, 1992, *R. chucunaque* Breder, 1925, *R. cryptocallus* Seegers & Huber, 1981, *R. deltaphilus* Seegers, 1983, *R. depressus* Costa, 1991, *R. derhami* Fels & Huber, 1985, *R. elegans* Steindachner, 1880, *R. elongatus* Fels & de Rham, 1981, *R. erberi* Berkenkamp, 1989, *R. frommi* Berkenkamp & Etzel, 1993, *R. fuscolineatus* Bussing, 1980, *R. glaucus* Bussing, 1980, *R. haraldsiolii* Berkenkamp, 1984, *R. hartii* (Boulenger, 1890), *R. hildebrandi* Myers, 1927, *R. holmiae* Eigenmann, 1909, *R. igneus* Huber, 1991, *R. immaculatus* Thomerson, Nico & Taphorn, 1991, *R. intermittens* Fels & de Rham, 1981, *R. iridescens* Fels & de Rham, 1981, *R. isthmensis* Garman, 1895, *R. janeiroensis* Costa, 1991, *R. jucundus* Huber, 1992, *R. kuelpmanni*

Berkenkamp & Etzel, 1993, *R. lanceolatus* Eigenmann, 1909, *R. leucurus* Fowler, 1944, *R. limoncochae* Hoedeman, 1962, *R. luelingi* Seegers, 1984, *R. lungi* Berkenkamp, 1984, *R. magdalenae* Eigenmann & Henn, 1916, *R. mazaruni* Myers, 1924, *R. micropus* (Steindachner), 1863, *R. monikae* Berkenkamp & Etzel, 1995, *R. monticola* Staeck & Schindler, 1997, *R. montium* Hildebrand, 1938, *R. nudiventris* Costa & Brasil, 1991, *R. ophiomimus* Huber, 1992, *R. pacificus* Huber, 1992, *R. peruanus* (Regan, 1903), *R. rubripunctatus* Bussing, 1980, *R. rubrolineatus* Fels & de Rham, 1981, *R. santensis* Köhler, 1906, *R. siegfriedi* Bussing, 1980, *R. simplicis* Costa, 2004, *R. speciosus* Fels & de Rham, 1981, *R. stagnatus* Eigenmann, 1909, *R. sucubti* Breder, 1925, *R. taeniatus* Fowler, 1945, *R. tenuis* (Meek, 1904), *R. tessellatus* Huber, 1992, *R. uroflammeus* Bussing, 1980, *R. urophthalmus* Günther, 1866, *R. villwocki* Berkenkamp & Etzel, 2002, *R. waimacui* Eigenmann, 1909, *R. wassmanni* Berkenkamp & Etzel, 1999, *R. weberi* Huber, 1992, and *R. xanthonotus* Ahl, 1926.

Distribution

River basins of Mesoamerica (between Mexico and Panama, and southern Caribbean islands), and northern (Colombia, Venezuela, Guianas, Peru, Ecuador, Bolivia and northern Brazil) and eastern South America (coastal plains of south, south-eastern and north-eastern Brazil).

Rivulus urophthalmus Günther, 1866

(Figs 2-9; Table 1)

Rivulus urophthalmus Günther, 1866: 327 (type locality: Para [Belém, formerly often known as Pará, northern Brazil]; lectotype: BMNH 1851.12.26, designated by Huber 1991:67; photograph of lectotype in Huber 1991: 72, fig. 7).

Rivulus poey Steindachner, 1876: 165 (type locality: canals in the city of Para [now Belém]; types unknown; neotype: UFRJ 6282, male, 34.9 mm SL; creek at 15 de agosto street, Icoaraci, Belém; collected by A. Sarraf & M. Mourão Jr., 24 Jul. 1996 [herein designated]).

Rivulus urophthalmus var. *aurata* Schreitmüller, 1928: 88 (Maharankao [correctly Maranhão], Brazil; type: not designated).

Material examined

Brazil: Estado do Pará: UFRJ 6247, 18; stream in praia de Ariramba, ilha do Mosqueiro, Belém,

1°6'34.7"S 48°25'32.7"W; W. J. E. M. Costa, R. Paiva & D. Ramos, 21 Jun. 2004. UFRJ 6248, 11; stream in ilha do Mosqueiro, Belém, 1°9'27.4"S 48°20'55.4"W; W. J. E. M. Costa, R. Paiva & D. Ramos, 21 Jun. 2004. UFRJ 6254, 8; UFRJ 6261, 3; stream crossing the road PA-391, ilha do Mosqueiro, Belém, 1°8'59.5"S 48°21'27.9"W; W. J. E. M. Costa, R. Paiva & D. Ramos, 21 Jun. 2004. UFRJ 6255, 11; creek near the road PA-124, near Santa Luzia, 0°46'39.1"S 47°16'43.5"W; W. J. E. M. Costa, R. Paiva & D. Ramos, 19 Jun. 2004. UFRJ 6256, 5; pools near stream near the road PA-446, Primavera, 0°54'8.9"S 47°2'31.0"W; W. J. E. M. Costa, R. Paiva & D. Ramos, 18 Jun. 2004. UFRJ 6257, 9; swamp at Quatipuru, 0°52'12.4"S 47°0'23.6"W; W. J. E. M. Costa, R. Paiva & D. Ramos, 18 Jun. 2004. UFRJ 6258, 15; stream near the road PA-124, near Pindorama, Salinópolis, 0°42'28.1"S 47°18'5.6"W; W. J. E. M. Costa, R.

Paiva & D. Ramos, 18 Jun. 2004. UFRJ 6259, 4; UFRJ 6290, 34; stream at forest edge, road PA-446, Primavera, 0°56'23.9"S 47°5'21.6"W; W. J. E. M. Costa, R. Paiva & D. Ramos, 19 Jun. 2004. UFRJ 4087, 9 (c&s); igarapé Maguary, Belém; A. Sarraf & E. Nogueira, 1 Aug. 1996. UFRJ 3055, 6 (c&s); Primavera; A. Werner, May 1988. UFRJ 4082, 6; campus of Universidade Federal do Pará, Belém; A. Sarraf & M. Mourão Jr., 30 Jul. 1996. UFRJ 4083, 4; creek at 15 de agosto street, Icoaraci, Belém; A. Sarraf & E. Nogueira, 1 Aug. 1996. UFRJ 4079, 5; igarapé Maguary, Belém; A. Sarraf & M. Mourão Jr., 24 Jul. 1996. Estado do Tocantins: UFRJ 5149, 9; floodplains of left bank of rio Tocantins, about 1200 m from the river margin, SSE Sampaio, 5°23'00"S 47°51'41"W; G. C. Brasil, 8 Jun. 2000. UNT 553, 3; rio Brejão, road BR-153, Araguaína; E. L. Beerli & L. M. Lima, 22 Nov. 2003. UNT 554, 5; river at the road BR-153, between Filadel-



Fig. 2. *Rivulus urophthalmus*, UFRJ 6261, male, 27.1 mm SL (two days after collection); Brazil: Pará: Belém. Photo by W. J. E. M. Costa.



Fig. 3. *Rivulus urophthalmus*, UFRJ 6261, male, 26.7 mm SL (two days after collection); Brazil: Pará: Belém (same population as Fig. 3, with slightly different colour patterns on the caudal fin). Photo by W. J. E. M. Costa.



Fig. 4. *Rivulus urophthalmus*, UFRJ 6261, female, 30.0 mm SL (two days after collection); Brazil: Pará: Belém. Photo by W. J. E. M. Costa.



Fig. 5. *Rivulus urophthalmus*, UFRJ 6259, male, 30.1 mm SL (one day after collection); Brazil: Pará: Primavera. Photo by W. J. E. M. Costa.

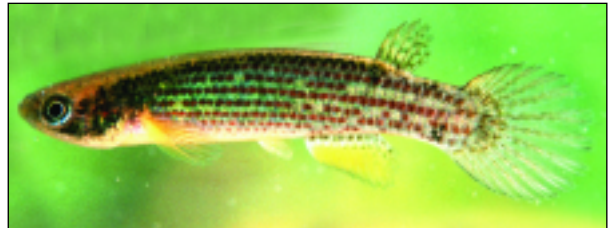


Fig. 6. *Rivulus urophthalmus*, UFRJ 6256, male, 26.6 mm SL (one day after collection); Brazil: Pará: Primavera (compare with Fig. 5 to observe different colour patterns on the caudal peduncle). Photo by W. J. E. M. Costa.



Fig. 7. *Rivulus urophthalmus*, UFRJ 6259, female, 33.2 mm SL (one day after collection); Brazil: Pará: Primavera. Photo by W. J. E. M. Costa.

phia and Araguaia; E. L. Beerli, 2 Nov. 2003. Estado do Amapá: INPA 2244, 26 (3 c&s); stream below cachoeira Santo Antônio, rio Jari drainage; M. Jegu & J. Zuanon, 21 Jun. 1987. Estado do Maranhão: UFRJ 5152, 16; swamp about 500 m from the right margin of rio Tocantins, 5°12'33"S 48°27'59"W; G. C. Brasil, 8 Jun. 2000. UFRJ 6293, 4; Olho d'Água das Cunhãs; A. C. De Luca, C. G. C. Wenceslau & M. A. Santos, 7 Jul. 2003.

Diagnosis

Distinguished from all other congeners by the combination of the following features: anterior portion of trunk slightly deeper than wide, jaws short,



Fig. 8. *Rivulus urophthalmus*, UFRJ 6264, male, 29.5 mm SL (one day after collection); Brazil: Pará: Altamira. Photo by W. J. E. M. Costa.

snout blunt, tip of anal fin rounded in male, caudal fin rounded in male, pelvic-fin tip not reaching anus in male, dorsal-fin origin on vertical between base of last 3rd and 4th anal-fin rays, dorsal-fin rays 7-8, anal-fin rays 12-14, frontal squamation E-patterned, frontal scales arranged circularly, canal preopercular short and opened, contact organs absent, longitudinal series of scales 37-40, gill rakers of first branchial arch 1-2 + 8, red stripes on flank, jaws not distinctively pigmented, and round black spot on dorsal portion of caudal fin in female.

Description

Morphometric data appear in Table I. Largest spec-



Fig. 9. *Rivulus urophthalmus*, UFRJ 6264, female, 28.9 mm SL (one day after collection); Brazil: Pará: Altamira. Photo by W. J. E. M. Costa.

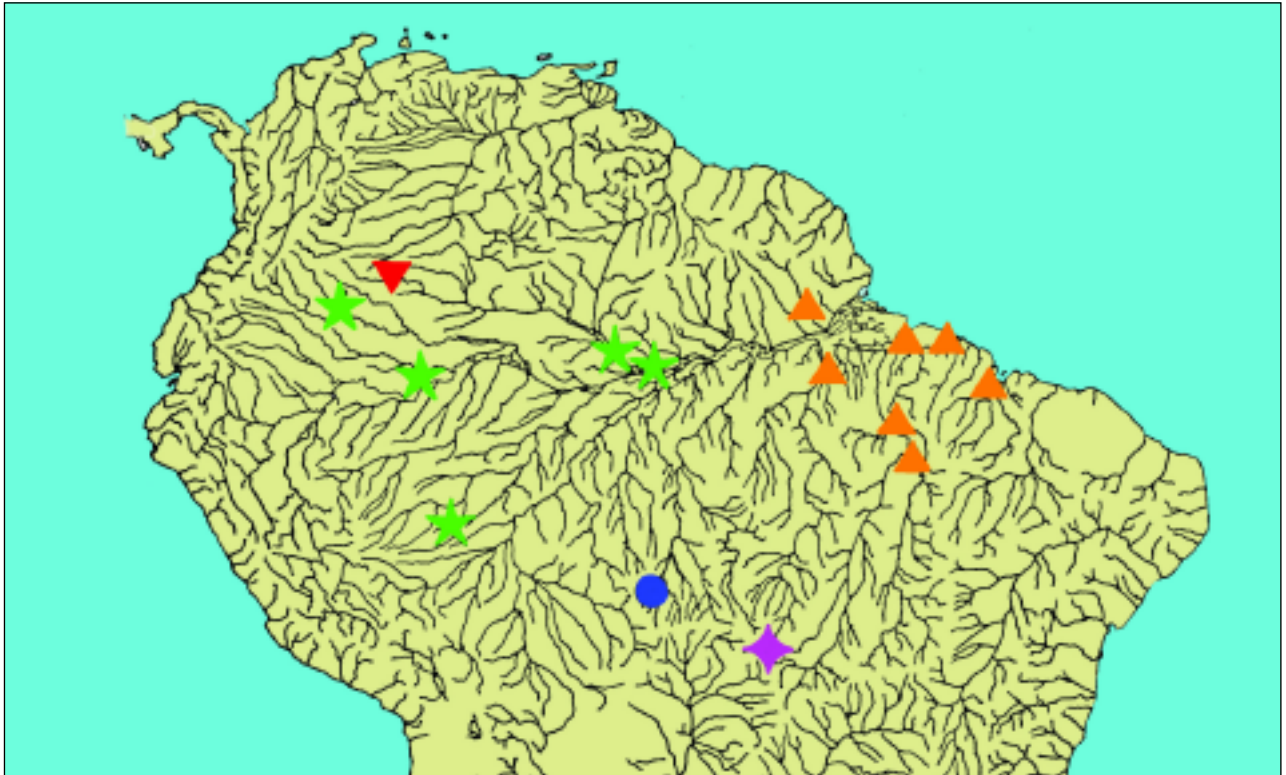


Fig. 10. Geographic distribution of: *Rivulus modestus* (dot), *R. romeri* (inverted triangle), *R. taeniatus* (stars), *R. urophthalmus* (triangles), and *R. violaceus* (lozenges). One symbol may represent more than one collecting site.

imen, a female 43.9 mm SL. Dorsal profile gently convex from snout to end of dorsal-fin base, approximately straight on caudal peduncle. Ventral profile slightly convex from lower jaw to end of anal-fin base, about straight on caudal peduncle. Body slender, subcylindrical anteriorly, slightly deeper than wide, to compressed posteriorly. Greatest body depth at vertical just in front to pelvic-fin base. Jaws short, snout blunt.

Tip of dorsal and anal fins rounded. Caudal fin rounded. Pectoral fin short and rounded, posterior margin reaching vertical at about 60% of length between pectoral-fin and pelvic-fin bases. Pelvic fin short and elliptical, tip not reaching anus. Pelvic-fin bases medially separated by short interspace. Dorsal-fin origin on vertical between base of 3rd and 4th last anal-fin rays, and between neural spines of 21st and 23rd vertebrae. Anal-fin origin between pleural ribs of 15th and 17th vertebrae. Dorsal-fin rays 7-8; anal-fin rays 12-14; caudal-fin rays 25-28; pectoral-fin rays 13; pelvic-fin rays 6.

Scales small, cycloid. Body and head entirely scaled, except anterior ventral surface of head. Body squamation extending over anterior 30 % of caudal-fin base; no scales on dorsal- and anal-fin bases. Frontal squamation E-patterned; E-scales not overlapping medially; scales arranged in regular circular pattern around A-scale without exposed margins. Longitudinal series of scales 37-40; transverse series of scales 8; scale rows around caudal peduncle 16. Contact organs absent.

Cephalic neuromasts: supraorbital 3 + 3, parietal 1, anterior rostral 1, posterior rostral 1, infraorbital 1 + 1 + 11-15 + 1, preorbital 2-3, otic 1, post-otic 2, supratemporal 1, median opercular 1, ventral opercular 2, preopercular 2 + 4, mandibular 4 + 1, lateral mandibular 2-3.

Interhyal minute, cartilaginous. Rostral cartilage longer than wide, width about 80% length. Basihyal subtriangular, width about 65% length; basihyal cartilage about 10% basihyal length. Six branchiostegal rays. Second pharyngobranchial teeth 3-4. Gill rakers of first branchial arch 1-2 + 8. Vomerine teeth 5-6. Ventral process of posttemporal short. Total vertebrae 32-35.

Coloration in life: Male: Side of body metallic yellowish green to metallic purplish blue ventrally; eight longitudinal rows of red to reddish brown dots, often in close proximity, forming stripes; usually three, sometimes four or five rows of red dots crossing caudal peduncle and reaching caudal-fin base, remaining rows reaching vertical through anal-

fin base; dark chromatophores concentrated on longitudinal zone between flank and dorsum; sometimes dark grey bars on flank anterior to caudal peduncle, when fish exposed to strong sunlight. Dorsum light brown. Venter white. Side of head metallic yellowish green to metallic purplish blue, sometimes dark grey when fish exposed to strong sunlight. Lower jaw light brown. Iris light yellowish to greenish brown. Dorsal fin pale yellow with brown dots on basal portion, often with bright yellow zone. Anal fin yellow, basal portion sometimes blue, often with brown or red dots. Caudal fin pale yellow, often with brown dots and dorsal and ventral bright yellow zones, sometimes dorsal and ventral margins bright orange. Paired fins yellowish hyaline.

Female: Side of body light brown, with eight longitudinal rows of reddish brown dots, often in close proximity, forming stripes, alternating with longitudinal rows of pale golden dots; dark chromatophores concentrated on longitudinal zone between flank and dorsum; sometimes dark grey bars on flank anterior to caudal peduncle, when fish exposed to strong sunlight. Dorsum light brown. Venter white. Side of head pale metallic yellowish green to metallic purplish blue, sometimes dark grey when fish exposed to strong sunlight. Lower jaw light brown. Iris light yellowish to greenish brown. Unpaired fins yellowish hyaline with brown dots; round black spot on dorsal portion of caudal fin usually reaching fin margin, anteriorly bordered by small, triangular pale yellow spot. Paired fins hyaline.

Distribution

Lower Amazon basin, including lower Xingu and



Fig. 11. Brazil: Pará: Primavera; pool close to creek near forest border, typical habitat of *Rivulus urophthalmus*. Photo by W. J. E. M. Costa.

Table I. Morphometric data of the *R. urophthalmus*, *R. taeniatus*, *R. micropus*, and *R. ornatus*.

	<i>R. urophthalmus</i>		<i>R. taeniatus</i>		<i>R. micropus</i>		<i>R. ornatus</i>	
	males (10)	females (10)	males (10)	females (10)	males (6)	females (4)	males (5)	females (4)
Standard length (mm)	26.7-34.9	24.9-35.4	29.7-61.1	28.8-50.1	31.9-42.8	30.8-41.8	19.4-21.1	19.3-19.7
Percents of standard length								
Body depth	19.6-21.9	19.5-21.9	18.7-20.9	18.6-21.7	18.0-19.6	17.0-19.0	17.4-19.0	16.6-18.4
Caudal peduncle depth	12.5-13.9	12.7-13.4	12.6-16.0	12.6-14.3	12.9-14.1	12.4-13.4	12.7-14.4	12.5-13.4
Pre-dorsal length	77.0-79.1	76.2-78.8	78.0-79.9	78.6-80.8	77.7-80.6	77.9-81.1	78.5-81.7	81.0-84.6
Pre-pelvic length	53.1-55.0	53.3-55.8	53.6-57.7	54.5-57.5	50.5-54.5	52.5-53.9	53.3-57.0	53.6-57.3
Length of dorsal-fin base	7.0-9.1	7.1-8.5	6.1-8.5	6.5-8.5	6.1-8.1	6.1-8.3	6.2-7.8	5.0-6.1
Length of anal-fin base	16.7-19.3	16.0-18.7	16.6-18.7	16.3-19.1	16.3-18.7	15.5-17.6	14.0-16.4	13.3-15.2
Caudal-fin length	30.4-36.2	33.1-37.4	29.0-33.3	29.0-32.4	30.4-36.2	31.4-33.3	46.0-51.6	44.7-45.8
Pectoral-fin length	17.4-19.7	17.1-20.9	17.0-20.0	16.7-19.6	18.9-20.7	18.0-19.3	22.1-26.3	22.5-23.6
Pelvic-fin length	8.0-10.0	7.7-8.9	7.9-10.6	7.1-9.1	9.9-13.4	9.2-10.0	11.5-14.1	10.4-12.1
Head length	23.0-25.4	23.1-26.2	22.8-24.8	23.0-24.9	24.4-25.3	24.3-25.6	27.0-28.6	27.8-28.1
Percents of head length								
Head depth	63.7-71.2	64.5-73.7	64.1-73.8	64.7-74.5	57.5-60.3	54.7-58.6	51.4-55.7	48.8-53.6
Head width	75.6-82.9	77.9-85.7	78.2-91.8	78.7-88.3	72.8-74.4	71.4-77.4	73.6-79.6	73.3-80.0
Snout length	13.1-16.8	13.9-17.2	13.0-17.0	13.9-15.8	14.8-15.1	13.9-14.2	11.5-14.3	12.0-13.5
Lower jaw length	19.5-23.2	20.8-25.3	23.3-25.5	23.1-26.1	22.8-24.2	24.6-27.0	20.2-22.8	19.1-20.3
Eye diameter	30.5-34.5	29.3-34.5	28.4-36.7	28.0-34.9	30.4-32.1	28.4-32.0	28.6-34.1	28.5-33.5

Tocantins river basins, and adjacent coastal drainages to East, northern Brazil (Fig. 10).

Habitat

Shallow creeks at sunny places, sometimes in forest border, at depths of about 5-10 cm (Fig. 11).

Rivulus taeniatus Fowler, 1945

(Figs 12-16; Table I)

Rivulus taeniatus Fowler, 1945: 129 (type locality: Morelia, río Caqueta drainage, Colombia; holotype: ANSP 71720, illustrated by Fowler 1945: 129).

Material examined

Brazil: Estado do Amazonas: UFRJ 6245, 23; UFRJ 6246, 4 (c&zs); creek adjacent to rio Urubuí, rio Urubu basin, Presidente Figueiredo, 2°2'43.9"S 60°1'43.2"W; W. J. E. M. Costa, R. Paiva & D. Ramos, 11 Jun. 2004. INPA 1847, 1; INPA 1848, 2; pool near igarapé Acará, Reserva Ducke, Manaus; Rosa, 23 Mar. 1988. INPA 2367, 4; Belém dos Palmares, rio Solimões, between Benjamin Constant and São Paulo de Olivença; R. Silva, 1 May 1987. INPA 3905, 3; INPA 3906, 1; igarapé Candiru, km 50 of the Manaus-Itacoatiara road; C. Pereira, 11 Jul. 1990. UFRJ 3931, 73; pool near igarapé Acará, Reserva Ducke, Manaus; C. Figueiredo & C. Codeço, 21 Sep. 1996. Estado do Acre: ZUEC non catalogued, 4; Campus Cacimba; C. F. D. Haddad

& J. R. Santos, 2 Jan. 1982. UFRJ 6291, 7; UFRJ 6292, 82; creek between Rio Branco and Senador Guiomard, rio Acre drainage; W. J. E. M. Costa *et al.*, 12 Jun. 2003.

Diagnosis

Distinguished from all other congeners by the combination of the following features: anterior portion of trunk slightly deeper than wide, jaws short, snout blunt, tip of anal fin rounded in male, caudal fin rounded in male, pelvic-fin tip usually not reaching anus and never reaching the anterior portion of the anal-fin base in male, dorsal-fin origin on vertical between base of last 2nd and 3rd anal-fin rays, dorsal-fin rays 7-9, anal-fin rays 12-15, frontal squamation E-patterned, frontal scales arranged circularly, canal preopercular short and opened, contact organs on flank scales in male, longitudinal series of scales 38-40, gill rakers of first branchial arch 2 + 9, red stripes on flank, jaws not distinctively pigmented



Fig. 12. *Rivulus taeniatus*, UFRJ 6246, male, 31.6 mm SL (minutes after collection); Brazil: Amazonas: Presidente Figueiredo. Photo by W. J. E. M. Costa.

except by red tip of lower jaw, and round black spot on dorsal portion of caudal-fin in female.

Description

Morphometric data appear in Table I. Largest specimen, a male 61.1 mm SL. Dorsal profile gently convex from snout to end of dorsal-fin base, approximately straight on caudal peduncle. Ventral profile slightly convex from lower jaw to end of anal-fin base, about straight on caudal peduncle. Body slender, subcylindrical anteriorly, slightly deeper than wide, to compressed posteriorly. Greatest body depth at vertical just in front to pelvic-fin base. Jaws short, snout blunt.

Tip of dorsal and anal fins rounded. Caudal fin rounded. Pectoral fin short and rounded, posterior margin reaching vertical at about 60 % of length between pectoral- and pelvic-fin bases. Pelvic fin short and elliptical, often tip not reaching anus, sometimes on urogenital papilla in male. Pelvic-fin bases medially separated by short interspace. Dorsal-fin origin on vertical between base of last 2nd and 3rd anal-fin rays, and between neural spines of 21st and 23rd vertebrae. Anal-fin origin between pleural ribs of 15th and 16th vertebrae. Dorsal-fin rays 7-9; anal-fin rays 12-15; caudal-fin rays 27-28; pectoral-fin rays 13-14; pelvic-fin rays 7.

Scales small, cycloid. Body and head entirely

scaled, except anterior ventral surface of head. Body squamation extending over anterior 30 % of caudal-fin base; no scales on dorsal and anal-fin bases. Frontal squamation E-patterned; E-scales not overlapping medially; scales arranged in regular circular pattern around A-scale without exposed margins. Longitudinal series of scales 38-40; transverse series of scales 8; scale rows around caudal peduncle 16-18. Contact organ on each scale of midventral ventral portion of flank in male.

Cephalic neuromasts: supraorbital 3 + 3, parietal 1, anterior rostral 1, posterior rostral 1, infraorbital 1 + 1 + 13-15 + 1, preorbital 2-3, otic 1, post-otic 2, supratemporal 1, median opercular 1, ventral opercular 2, preopercular 2 + 4, mandibular 3-4 + 1, lateral mandibular 2.

Interhyal minute, cartilaginous. Basihyal subtriangular, width about 55 % length; basihyal cartilage about 10 % basihyal length. Six branchiostegal rays. Second pharyngobranchial teeth 1. Gill rakers of first branchial arch 2 + 9. Vomerine teeth 1. Ventral process of posttemporal short. Total vertebrae 33-36.

Coloration in life: Male: Side of body metallic yellowish green to metallic purplish blue ventrally; 7-8 longitudinal rows of red to reddish brown dots, usually in close proximity, forming stripes; usually three, sometimes four or five rows of red dots crossing cau-

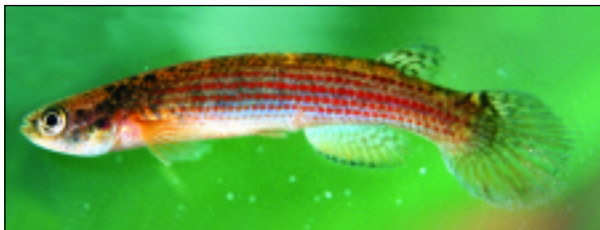


Fig. 13. *Rivulus taeniatus*, UFRJ 6246, female, 33.3 mm SL (minutes after collection); Brazil: Amazonas: Presidente Figueiredo. Photo by W. J. E. M. Costa.

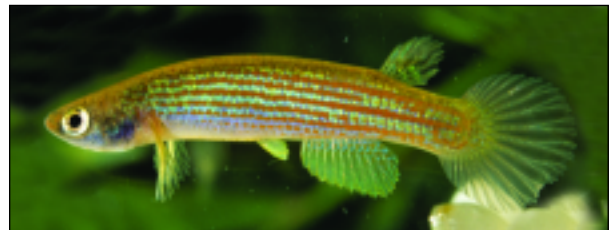


Fig. 14. *Rivulus taeniatus*, UFRJ 6291, male, 28.1 mm SL (one day after collection); Brazil: Acre: Rio Branco. Photo by W. J. E. M. Costa.

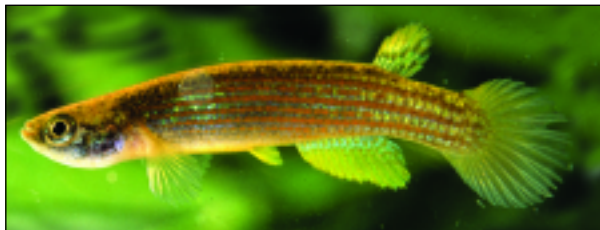


Fig. 15. *Rivulus taeniatus*, UFRJ 6291, male, 28.5 mm SL (one day after collection); Brazil: Acre: Rio Branco (compare to Fig. 14 to observe slightly different pigmentation patterns in individuals of the same population). Photo by W. J. E. M. Costa.



Fig. 16. *Rivulus taeniatus*, UFRJ 6291, female, 30.9 mm SL (one day after collection); Brazil: Acre: Rio Branco. Photo by W. J. E. M. Costa.