

## Two new species of the *Rivulus urophthalmus* group from the Tocantins and Xingu river drainages, eastern Brazilian Amazon (Cyprinodontiformes: Rivulidae)

Wilson J. E. M. Costa\*

*Rivulus tocantinensis*, new species, from the middle section of the Tocantins River drainage, and *R. xinguensis*, new species, from the lower Xingu River drainage, eastern Amazonas River basin, northern Brazil, are described. Both species are missing the well-defined marginal yellow stripes on the caudal fin present in adult males of all other species of the *R. urophthalmus* group. *Rivulus tocantinensis* is distinguished from all other species of the *R. urophthalmus* group in having wide dark orange stripes on the flank and large dark orangish brown blotches on the middle of the caudal fin in males, and the absence of dermosphenotic bone or sometimes represented by a rudimentary ossification; *R. xinguensis* differs from other species of that group in having fewer scales in the longitudinal series.

*Rivulus tocantinensis*, sp. nov., da seção média da drenagem do rio Tocantins, e *R. xinguensis*, sp. nov., da drenagem do baixo rio Xingu, leste da bacia do rio Amazonas, norte do Brasil, são descritas. Ambas as espécies não possuem as bem-definidas faixas amarelas marginais presentes em machos adultos de todas as outras espécies do grupo *R. urophthalmus*. *Rivulus tocantinensis* se distingue de todas as outras espécies do grupo *R. urophthalmus* por possuir largas faixas alaranjadas no flanco e grandes manchas castanho alaranjadas escuras no meio da nadadeira caudal em machos, e pela ausência do osso dermosfenótico ou algumas vezes representado por uma ossificação rudimentar; *R. xinguensis* difere de outras espécies daquele grupo por possuir menos escamas na série longitudinal.

### Introduction

Species of the New World aplocheiloid genus *Rivulus* constitute a geographically widespread assemblage, not diagnosed by unique apomorphic features (e.g., Costa, 2006). This diversified possibly non-monophyletic assemblage (e.g., Murphy et al., 1999), with more than 125 valid species, has been tentatively divided into species groups

(e.g., Huber, 1992) or subgenera (e.g., Costa, 2006). Whereas most proposed subgenera of *Rivulus* are supported both by morphological and genetic features (Costa, 2006), some less inclusive species groups may not comprise monophyletic units. This is the case of Huber's (1992) *R. urophthalmus* species group (originally proposed as a superspecies), diagnosed by a combination of character states of uncertain polarity. Seven species were

\* Laboratory of Systematics and Evolution of Teleost Fishes, Instituto de Biologia, Universidade Federal do Rio de Janeiro, Caixa Postal 68049, CEP 21944-970, Rio de Janeiro, RJ, Brasil. E-mail: wcosta@biologia.ufrj.br

included in the *R. urophthalmus* group (Huber, 1992): *R. urophthalmus* from the lower Amazonas River basin, *R. stagnatus*, *R. mazaruni* and *R. lungi* from the Guianas, *R. deltaphilus* from the lower Orinoco basin in Venezuela, and *R. taeniatus* and *R. rubrolineatus*, from the western Amazonian basin in Colombia and Peru. However, the two latter species seems to be better placed in another species group, named as the *R. limoncochae* group by Huber (1992) to include four other species from the western Amazon: *R. christinae*, *R. limoncochae*, *R. iridescens* and *R. erberi*.

Both the *urophthalmus* and *limoncochae* groups were diagnosed by a combination of similar character states (e.g., longitudinal rows of red spots on flank, frontal squamation E-patterned, short dorsal and anal fins [i. e., dorsal fin with 6-9 rays, anal fin with 12-15 rays], long pre-dorsal distance, and large caudal spot in females) (Huber, 1992), the *R. limoncochae* group differing from the *R. urophthalmus* group by having three rows of red spots or stripes posteriorly extending to caudal-fin base (vs. six to eight in the *R. urophthalmus* group). However, as discussed by Costa (2006), species of the *R. urophthalmus* group may also have that condition, but species of the *R. urophthalmus* group (excluding *R. taeniatus* and *R. rubrolineatus*) may be distinguished from species of the *R. limoncochae* group (also including *R. taeniatus*, *R. rubrolineatus*, *R. christinae*) by males of the latter group having contact organs on scales of the flank (vs. absence) and an oblique transverse stripe on the middle of the dorsal fin (vs. absence), and by the absence of similar light yellow to orange zones on dorsal and ventral margins of the caudal fin (vs. presence).

Costa (2006) redescribed *R. urophthalmus* on the basis of specimens collected at the type locality, Belém, and adjacent Amazonian areas, but also listed specimens collected in the middle Tocantins River basin among the material examined, which were poorly preserved. In addition, Costa provided photographs of living individuals from the floodplains of the Xingu River, which were tentatively identified as *R. urophthalmus*. A further analysis of morphological characters of all populations previously identified as *R. urophthalmus*, including examination of living individuals and well preserved specimens recently collected in the middle Tocantins River basin, supported the recognition of the populations from the Tocantins and Xingu basins as two distinct species, which are herein described.

## Material and methods

Morphological characters were obtained from specimens fixed in formalin just after collection, for a period of 10 days, and then transferred to 70 % ethanol. Exceptions were specimens kept alive for one or two days, which were photographed in life. Material is deposited in the ichthyological collection of the Instituto de Biologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro (UFRJ).

Descriptions of color patterns were based both on direct examination of live specimens in the field just after collection, in small recipients with translucent walls, and photographs of both sides of some live individuals (usually three males and two females) of each population taken in aquaria between two and 48 hours after collection, then fixed as described above.

Measurements and counts follow Costa (1995); a complete set of measurements were made only in specimens adequately preserved, avoiding errors due to bad fixation (e.g., specimens with twisted body). Measurements are presented as percent of standard length (SL), except for those related to head morphology, which are expressed as percent of head length. Fin-ray counts include all elements. Number of vertebrae and gill-rakers were recorded from cleared and stained specimens; the compound caudal centrum was counted as a single element.

Osteological preparations (c&s) were made according to Taylor & Van Dyke (1985), but most specimens were not stained for cartilages to avoid ossification damage produced by the acetic acid present in the Alcian Blue solution. Terminology for bones follows Costa (2006), for frontal squamation Hoedeman (1958) and for cephalic neuromast series Costa (2001).

Delimitation of species follows the methodology of the Population Aggregation Analysis formally described by Davis & Nixon (1992), which is the foundation for the Phylogenetic Species Concept (e.g., Nixon & Wheeler, 1990; Wheeler & Platnick, 2000). Species are delimited by a unique combination of stable morphological character states in one or more populations, which is considered as evidence of absence of gene flow between the proposed delimited species and their congeners.



Fig. 1. *Rivulus tocantinensis*, UFRJ 6676, male, holotype, 38.4 mm SL; Brazil: Pará: Sampaio (two days after collection).

*Rivulus tocantinensis*, new species  
(Fig. 1)

**Holotype.** UFRJ 6676, male, 38.4 mm SL; Brazil: Estado do Tocantins: Município de Sampaio: stream 4 km of city of Sampaio, floodplains of left bank of Tocantins River, 5°23'00" S 47°51'41" W; G. C. Brasil, 21 Feb 2008.

**Paratypes.** UFRJ 6584, 7 males, 28.9-37.6 mm SL, and 5 females, 31.7-33.7 mm SL; UFRJ 6585, 2 males, 25.2-29.4 mm SL, and 2 females, 25.2-29.5 mm SL; UFRJ 6683, 3 males, 26.0-34.8 mm SL, and 1 female, 21.8 mm SL (c&s); UFRJ 6685, 1 female; 30.9 mm SL; collected with holotype.

**Diagnosis.** Distinguished from all other species of the *R. urophthalmus* group by the dermosphenotic being absent or sometimes rudimentary (vs. present and always well-developed), and by the presence of brownish orange stripes wider than interspace on the flank in males (vs. longitudinal rows of dark red to reddish brown dots, sometimes coalesced to form stripes narrower than interspace) and large dark orangish brown blotches on the middle of the caudal fin in males (vs. blotches always absent). Also distinguished from *R. urophthalmus*, *R. stagnatus*, *R. mazaruni*, *R. lungi* and *R. deltaphilus* by the absence of a well-defined yellow stripe on the upper and lower margins of the caudal fin in males (vs. presence); and, from *R. urophthalmus*, by the absence of diffuse dark gray bars on anterior portion of the flank in males (vs. presence).

**Description.** Morphometric data appear in Table 1. Largest male examined 38.4 mm SL; largest female examined 33.7 mm SL. Dorsal profile slightly convex, almost straight, from snout to end of dorsal-fin base, approximately straight on caudal peduncle. Ventral profile gently convex from lower jaw to anal-fin origin, nearly straight along caudal peduncle. Body slender, subcylindrical anteriorly, slightly deeper than wide, to compressed posteriorly. Greatest body depth just anterior to pelvic-fin base. Jaws short, snout blunt.

Extremity of dorsal and anal fins rounded in both sexes. Caudal fin elliptical. Pectoral fin rounded, its posterior margin reaching vertical of anterior to pelvic-fin base, about 60 % of distance between bases of pectoral and pelvic fins. Pelvic fin short, tip reaching between anus and urogenital papilla in males, anterior to anus in females. Pelvic-fin bases medially in contact. Dorsal-fin origin in vertical through base of 10th or 11th anal-fin rays, between neural spines of 20th and 22nd vertebrae. Anal-fin origin between pleural ribs of 14th and 16th vertebrae. Dorsal-fin rays 7-8; anal-fin rays 12-14; caudal-fin rays 26-29; pectoral-fin rays 13-14; pelvic-fin rays 5-6.

Scales large, cycloid. Trunk and head entirely scaled. No scales on dorsal and anal-fin bases. Scales extending over anterior 40 % of caudal fin. Frontal squamation E-patterned, frontal scales circularly arranged around A-scale without free margins; E-scales not overlapping medially; supraorbital scales 5-6. Longitudinal series of scales 35-37; transverse series of scales 8; scale rows around caudal peduncle 16. No contact organ on

flank; rudimentary contact organs on second pectoral-fin ray in males.

Cephalic neuromasts: supraorbital 3+3, parietal 2, anterior rostral 1, posterior rostral 1, infraorbital 1+13-15+1, preorbital 2, otic 1, postotic 1, supratemporal 1, median opercular 1, ventral opercular 1-2, preopercular 2+4, mandibular 4+1, lateral mandibular 2-3, paramandibular 1. One neuromast per scale of lateral line, often absent. Two neuromasts on caudal-fin base.

Teeth conical; teeth on middle portion of outer row of dentary hypertrophied, strongly curved and laterally directed. Basihyal subtriangular, greatest width about 60 % of length; basihyal cartilage about 10 % of total basihyal length. Six branchiostegal rays. Two or three teeth on second pharyngobranchial. Gill-rakers on first branchial arch 1+8-9. Vomerine teeth 4-8. Dermosphenotic rudimentary or absent. Ventral process of posttemporal rudimentary or absent. Total vertebrae 32-33.

**Coloration.** Males. Side of body dark blue anteriorly and pale blue posteriorly, with seven brownish orange stripes wider than interspace, three of which between anterior part of flank and caudal-fin base and four stripes restricted to anterior part of flank; both brownish orange stripes

and blue interspace are sometimes interrupted by golden spots. Dorsum brown. Venter white. Side of head dark brown. Jaws brown. Iris light brown with green edge. Dorsal fin yellow with small brown spots on basal and posterior portions. Anal fin yellow, with small dark orange spots on basal portion. Caudal fin color ground pale yellow on dorsal and ventral portions, blue on middle, to dark gray on posterior and lower edge; dark orangish brown blotches on basal, middle and posterior portions of fin, more concentrated on fin rays. Pectoral fin yellowish hyaline. Pelvic fin yellow.

Females. Side of body light gray, with seven horizontal rows of small brown spots; few pale golden dots horizontally arranged. Dorsum light brown. Venter white. Side of head and jaws dark brown. Iris brown. Unpaired fins yellowish hyaline, with transverse rows of dark brown dots on dorsal and caudal fins, and two rows of reddish brown dots on anal-fin base; large, rounded black spot on dorsal portion of caudal-fin base, not contacting dorsal margin of fin. Paired fins hyaline.

**Distribution and habitat.** *Rivulus tocantinensis* is known only from the type locality, the floodplains of the left bank of the Tocantins River, near the city of Sampaio, Estado do Tocantins, Brazil. It

**Table 1.** Morphometric data of *Rivulus tocantinensis* and *R. xinguensis* (male ranges include holotype values).

	<i>Rivulus tocantinensis</i>			<i>Rivulus xinguensis</i>		
	holotype	males (n=8)	females (n=6)	holotype	males (n=5)	females (n=4)
Standard length (mm)	38.4	28.9-38.4	30.9-33.7	28.9	26.7-32.4	24.9-28.6
<b>Percents of standard length</b>						
Body depth	22.9	20.2-23.4	19.5-23.2	22.8	19.6-22.8	19.5-21.6
Caudal peduncle depth	15.5	13.8-15.5	13.1-14.6	15.4	12.5-15.4	12.7-14.0
Predorsal length	77.1	77.1-78.8	77.4-79.6	77.7	77.7-79.0	76.3-80.4
Prepelvic length	54.2	53.9-56.2	54.8-56.3	57.1	54.1-57.1	55.6-57.8
Length of dorsal-fin base	8.6	7.4-9.4	7.6-8.8	7.8	7.6-7.8	6.5-7.9
Length of anal-fin base	20.6	18.5-20.6	18.2-20.5	20.2	17.8-21.2	16.1-17.8
Caudal-fin length	34.6	33.8-36.5	33.7-36.2	39.0	34.0-39.6	35.9-39.6
Pectoral-fin length	20.9	20.2-23.3	18.8-21.3	21.3	18.5-21.4	19.4-21.3
Pelvic-fin length	8.3	8.3-10.2	7.9-9.1	9.9	8.2-9.9	8.2-9.9
Head length	24.4	23.6-25.7	23.2-26.2	25.4	23.2-25.4	24.9-26.2
<b>Percents of head length</b>						
Head depth	73.9	67.7-75.8	67.1-75.5	67.0	67.0-71.2	64.5-69.4
Head width	87.2	81.3-91.6	86.9-91.9	80.4	75.6-80.4	77.9-83.3
Snout length	16.0	13.4-16.7	13.1-16.4	12.7	12.7-16.8	15.4-17.4
Lower jaw length	25.7	22.4-27.5	21.5-24.9	23.7	20.7-23.7	20.8-23.8
Eye diameter	30.5	30.5-34.9	30.3-32.5	33.7	30.5-34.5	33.4-34.5

was collected in a small black-water stream within dense forest.

**Etymology.** The name *tocantinensis* refers to the occurrence of the new species in the Tocantins River basin.

*Rivulus xinguensis*, new species  
(Fig. 2)

**Holotype.** UFRJ 6686, male, 28.9 mm SL; Brazil: Estado do Pará: Município de Altamira: swamp close to left bank of Xingu River, near Altamira, 3°11'59" S 52°11'50" W; W. J. E. M. Costa, R. Paiva & D. Ramos, 16 Jun 2004.

**Paratypes.** UFRJ 6263, 4 males, 26.7-32.4 mm SL, and 3 females, 24.9-27.7 mm SL; UFRJ 6264, 1 female, 28.6 mm SL; UFRJ 6266, 2 males, 27.2-27.9 mm SL (c&s); collected with holotype.

**Diagnosis.** *Rivulus xinguensis* is distinguished from *R. urophthalmus*, *R. stagnatus*, *R. mazaruni*, *R. lungi* and *R. deltaphilus* in having 33-35 scales in the longitudinal series (vs. 36-43) and by the absence of well-defined yellow stripes on dorsal and anal margin of the caudal fin in males (vs. presence); from *R. urophthalmus*, by the absence of diffuse dark gray bars on anterior portion of the flank in males (vs. presence); and from *R. tocantinensis*, by having a well developed dermosphenotic (vs. absent, sometimes rudimentary), horizontal rows of small red spots on the flank in males (vs. wide brownish orange stripes), and transverse rows of dark brown dots on the caudal fin in males (vs. large dark orangish brown blotches on the middle of the caudal fin).

**Description.** Morphometric data appear in Table 1. Largest male examined 32.4 mm SL; largest female examined 28.6 mm SL. Dorsal and ventral profiles slightly convex, almost straight, from snout to end of dorsal and anal-fin bases, about straight on caudal peduncle. Body slender, subcylindrical anteriorly, slightly deeper than wide, to compressed posteriorly. Greatest body depth just anterior to pelvic-fin base. Jaws short, snout blunt.

Extremity of dorsal and anal fins rounded in both sexes. Caudal fin elliptical. Pectoral fin rounded, its posterior margin reaching vertical of anterior to pelvic-fin base, about 70 % of dis-

tance between bases of pectoral and pelvic fins. Pelvic fin short, tip reaching anus in males, anterior to anus in females. Pelvic-fin bases medially in close proximity. Dorsal-fin origin in vertical through base of 10th or 11th anal-fin rays, between neural spines of 20th and 22nd vertebrae. Anal-fin origin between pleural ribs of 14th and 16th vertebrae. Dorsal-fin rays 7-8; anal-fin rays 12-13; caudal-fin rays 26-28; pectoral-fin rays 13-14; pelvic-fin rays 6.

Scales large, cycloid. Trunk and head entirely scaled. No scales on dorsal and anal-fin bases. Scales extending over anterior 25-30 % of caudal fin. Frontal squamation E-patterned, frontal scales circularly arranged around A-scale without free margins; E-scales not overlapping medially; supraorbital scales 5-6. Longitudinal series of scales 33-35; transverse series of scales 8; scale rows around caudal peduncle 16. No contact organ on flank; rudimentary contact organs on second pectoral-fin ray in males.

Cephalic neuromasts: supraorbital 3+3, parietal 1, anterior rostral 1, posterior rostral 1, infraorbital 1+16+1, preorbital 2, otic 1, post-otic 1, supratemporal 1, median opercular 1, ventral opercular 2, preopercular 2+4, mandibular 4+1, lateral mandibular 2-3, paramandibular 1. One neuromast per scale of lateral line, often absent. Two neuromasts on caudal-fin base.

Teeth conical; teeth on middle portion of outer row of dentary hypertrophied, strongly curved and laterally directed. Basihyal subtriangular, greatest width about 55 % of length; basihyal cartilage about 20 % of total basihyal length. Six branchiostegal rays. One or two teeth on second pharyngobranchial. Gill-rakers on first branchial arch 1+8. Vomerine teeth 3. Dermosphenotic present. Ventral process of posttemporal rudimentary or absent. Total vertebrae 31-32.

**Coloration.** Males. Side of body pale blue, sometimes dark purplish blue on anterior portion, with seven horizontal rows of small dark red spots. Dorsum brown. Venter white. Side of head dark purplish brown. Upper jaw pale red, lower jaw brown. Iris light brown to bright green on ventral portion. Dorsal fin pale yellow with subproximal row of small brown dots. Anal fin yellow, with dark red dots on membrane of basal and posterior parts of fin. Caudal fin pale blue, lighter on upper and lower portions and slightly darker on posterior and lower edges, sometimes with narrow pale orange anterodorsal and anteroventral



Fig. 2. *Rivulus xinguensis*, UFRJ 6686, male, holotype, 28.9 mm SL; Brazil: Pará: Altamira (one day after collection).

margins; transverse rows of brown dots on middle of fin. Pectoral fin yellowish hyaline. Pelvic fin yellow.

Females. Side of body light brownish gray, with seven horizontal rows of small brown spots. Dorsum light brown. Venter white. Side of head and jaws dark brown. Iris brown. Dorsal and anal fins hyaline, both with transverse rows of dark brown dots; large, rounded black spot on upper portion of caudal-fin base, not contacting dorsal margin of fin. Anal fin yellowish hyaline, with two rows of reddish brown dots on basal portion. Paired fins hyaline.

**Distribution and habitat.** *Rivulus xinguensis* is only known from the type locality, a clear-water swamp area around a small creek near the left margin of the Xingu River, close to the city of Altamira, Pará, Brazil. It was collected in shallow parts of the swamp, about 10 cm deep. The specimens were found in parts of the swamp within dense rain forest.

**Etymology.** The name *xinguensis* is an allusion to the occurrence of the new species in the Xingu River basin.

### Discussion

The two species herein described are similar to *R. urophthalmus*, *R. stagnatus*, *R. mazaruni*, *R. lungi* and *R. deltaphilus* by the following combination of character states: longitudinal rows of red or orangish brown spots on flank in males, some-

times coalesced to form stripes; absence of contact organs on flank; dark bluish or purplish gray pigment over the side of the head in males; and, anal fin with 12-15 anal-fin rays. However, although presently useful to distinguish this group of species from all other congeners, the character states listed above have uncertain polarity, thus not serving to support monophyly of the *R. urophthalmus* species group.

Both *R. tocantinensis* and *R. xinguensis* are distinguished from *R. urophthalmus*, *R. stagnatus*, *R. mazaruni*, *R. lungi* and *R. deltaphilus* by the absence of a well-defined yellow stripe on the dorsal and ventral margins of the caudal fin in males. In *R. tocantinensis* and *R. xinguensis*, the dorsal and ventral portions of the caudal fin are lighter than the remaining parts of the fin, but do not form distinct stripes as in those five species. Well-defined yellow stripes are also found in *R. hartii*, from Trinidad-Tobago and the Venezuelan coastal plains, which is distinguished from species of the *R. urophthalmus* group by having more anal-fin rays (15-18 in *R. hartii* vs. 12-15 in species of the *R. urophthalmus* group). *Rivulus bahianus* from the coastal plains of northeastern Brazil has yellowish white stripes on the dorsal and ventral margins of the caudal fin in males; it differs from species of the *R. urophthalmus* group by having the side of the head light brown (vs. dark bluish or purplish gray extending over the whole side of the head). The latter condition is also present in several species of *Rivulus* from the western Amazonas River basin (e.g., *R. christinae*, *R. elongatus*, *R. iridescens*, *R. limoncochae*, *R. micropus*, and *R. rubrolineatus*) and some species from

the Caribbean islands and the coastal plains of Guiana and Venezuela (*R. hartii*, *R. cryptocallus*, and *R. holmiae*). *Rivulus tocantinensis* and *R. xinguensis* also differ from *R. urophthalmus* by the absence of diffuse dark gray bars on the anterior portion of the flank in males. The bars of *R. urophthalmus* are more conspicuous in live specimens exposed to sunlight and are not visible in preserved specimens.

*Rivulus tocantinensis* is easily distinguished from all other species of the *R. urophthalmus* group by the unique possession of brownish orange stripes wider than interspace on the flank in males and large dark orangish brown blotches on middle of the caudal fin in males. In addition, uniquely in *R. tocantinensis* the dermosphenotic is absent or sometimes only represented by a rudimentary ossification.

*Rivulus xinguensis* is distinguished from *R. urophthalmus*, *R. stagnatus*, *R. mazaruni*, *R. lungi* and *R. deltaphilus* in having fewer scales in the longitudinal series (33-35 vs. 36-43). A comparison between cleared and stained specimens of *R. xinguensis* and *R. urophthalmus* revealed that they also have distinct number of vertebrae (31-32 in *R. xinguensis* vs. 33-35 in *R. urophthalmus*). *Rivulus tocantinensis* has intermediate values: 35-37 scales in the longitudinal series and 32-33 vertebrae).

### Acknowledgements

I am grateful to R. Paiva and D. Ramos for help during collecting trips and to G. C. Brasil for collecting the type series of *R. tocantinensis*. The manuscript benefited from the criticisms by M. Kottelat. This study was supported by CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico – Ministério de Ciência e Tecnologia).

### Literature cited

- Costa, W. J. E. M. 1995. Pearl killifishes - the Cynolebiinae: systematics and biogeography of the neotropical annual fish subfamily. TFH, Neptune City, 128 pp.
- 2001. The neotropical annual fish genus *Cynolebias* (Cyprinodontiformes: Rivulidae): phylogenetic relationships, taxonomic revision and biogeography. *Ichthyological Exploration of Freshwaters*, 12: 333-383.
- 2006. Relationships and taxonomy of the killifish genus *Rivulus* (Cyprinodontiformes: Aplocheiloidei: Rivulidae) from the Brazilian Amazonas river basin, with notes on historical ecology. *Aqua Journal of Ichthyology and Aquatic Biology*, 11: 133-175.
- Davis, J. I. & K. C. Nixon. 1992. Populations, genetic variation, and the delimitation of phylogenetic species. *Systematic Biology*, 41: 421-435.
- Hoedeman, J. J. 1958. The frontal scalation pattern in some groups of toothcarps (Pisces, Cyprinodontiformes). *Bulletin of Aquatic Biology*, 1: 23-28.
- Huber, J. H. 1992. Review of *Rivulus*: ecobiogeography – relationships. *Société Française d'Ichtyologie*, Paris, 572 + 13 pp.
- Murphy, W. J., J. E. Thomerson & G. E. Collier. 1999. Phylogeny of the neotropical killifish family Rivulidae (Cyprinodontiformes, Aplocheiloidei) inferred from mitochondrial DNA sequences. *Molecular and Phylogenetic Evolution*, 13: 289-301.
- Nixon, K. C. & Q. D. Wheeler. 1990. An amplification of the phylogenetic species concept. *Cladistics*, 6: 211-223.
- Taylor, W. R. & G. C. Van Dyke. 1985. Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study. *Cybiurn*, 9: 107-109.
- Wheeler, Q. D. & N. I. Platnick. 2000. The phylogenetic species concept (sensu Wheeler & Platnick). Pp. 55-69 in Q. D. Wheeler & R. Meier (eds.), *Species concepts and phylogenetic theory: a debate*. Columbia University Press, New York.

Received 15 June 2009  
Revised 24 January 2010  
Accepted 27 January 2010