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Three new species of the killifish genus *Melanorivulus* from the Rio Paraná Basin, central Brazilian Cerrado (Cyprinodontiformes, Aplocheilidae)

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Abstract

Three new species of *Melanorivulus* are described from the upper and middle Rio Paraná Basin, central Brazilian Cerrado. These species are members of the *M. pictus* species group, endemic to central Brazilian plateaus and adjacent areas, and are easily diagnosed by colour pattern characters, but their relationships with other congeners of the group are still uncertain. *Melanorivulus proximus* **sp. n.**, from the middle Rio Aporé drainage, and *M. nigromarginatus* **sp. n.**, from the Rio Corrente drainage, are possibly more closely related to other species endemic to streams draining the slopes of the Caiapó range, whereas *M. linearis* **sp. n.**, from the upper Rio Pardo drainage, middle Rio Paraná Basin, is considered more closely related to *M. egens*, a species also endemic to this part of the Basin. This study corroborates the high diversity of species of *Melanorivulus* in the central Brazilian Cerrado plateaus repeatedly reported in previous studies, indicating once more that different species are often found restricted to short segments of the same river drainage. The intense habitat loss recorded in recent years combined to the high species diversity limited to specific Cerrado freshwater ecosystems, the veredas, indicates that species of *Melanorivulus* endemic to this part of the Brazilian Cerrado are highly threatened with extinction.

Introduction

The Cerrado savannas of central Brazil, with an area of about 2,000,000 km^2, is among the 25 most important biodiversity hotspots of the world (Myers et al. 2000). The present study is directed to a group of small killifishes of the genus *Melanorivulus* Costa, 2006, with species reaching 45 mm of standard length (SL) or less, inhabiting the shallowest parts of the veredas, a typical Cerrado ecosystem comprising streams bordered by the buriti-palm (*Mauritia flexuosa*). About 50 valid species are presently placed in *Melanorivulus*, formerly considered as a subgenus of *Rivulus* Poey, 1860 (Costa 2011). *Melanorivulus* is similar to other South American aplocheiloid killifishes living in similar biotopes, such as *Anablepsoides* Huber, 1992, *Atlantirivulus* Costa, 2008, *Cynodonichthys* Meek, 1904, *Laimosemion* Huber, 1999, *Rivulus* Poey, 1860, which have slender body, short fins and long neural prezygapophyses on caudal vertebrae (Costa 1990). Species of *Melanorivulus* are distinguishable from species of those 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, ventral process of the angulo-articular short or rudimentary, and preopercular canal absent (Costa 2011).

A great diversity of species of *Melanorivulus* has been reported for the Cerrado region drained by the Rio Paraná Basin, the second largest river basin in South America. A total of 14 endemic species have been described for this region (Costa 1989, 2005, 2007a, b, 2008; Nielsen et al. 2016; Volcan and Lanés 2017). These species belong to different and not closely related species groups (Costa et al. 2016): the *M. punctatus* group, containing slender small species, mainly diagnosed by the presence of oblique rows of red dots on the flank in males (e.g., Costa

2005); the *M. pinima* group, easily diagnosed by the reduction of black pigmentation on the head and humeral region in males, presence of longitudinal rows of red dots on the flank, and a longitudinally elongated white to light yellow mark above caudal spot in females (Costa 2007a), and the *M. pictus* group, diagnosed by a deeper body (i.e., body depth reaching about 25 % SL) and oblique red bars on the flank (Costa 2017). Eleven of the 14 endemic species are members of the last group, which are mostly concentrated in the rivers draining the Caiapó range and in the south adjacent areas of the middle Rio Paraná Basin (Costa 2005, 2012).

The *M. pictus* group was first studied by Costa (1989), based on fish collections deposited in the Museu de Zoologia, Universidade de São Paulo, when *M. apiamici* (Costa, 1989), *M. pictus* (Costa, 1989) and *M. vittatus* (Costa, 1989) were described. In September 1994, efforts were directed to firstly sample typical *Melanorivulus* habitats along the Paraná River Basin, but based on the great morphological variability found among populations inhabiting close neighbouring areas, Costa (1995) concluded that all populations of this vast geographical area belong to a single polymorphic species, *M. pictus*. However, after more accurate field studies since 2004, numerous new species have been continuously described for the Paraná and other adjacent river basins (e.g., Costa 2005, 2006, 2012, 2017; Deprá et al. 2017). These studies have indicated that each species is limited to small areas and that different species may inhabit the same river drainage at different altitudes (Costa 2007b, 2017; Volcan et al. 2017). However, some new species collected in recent years are still await formal descriptions. In this paper, three new species of the *M. pictus* group from the Paraná River Basin are described.

Materials and methods

Specimens were captured with small dip nets (40 × 30 cm) and fixed in formalin for a period of 10 days, and then transferred to 70 % ethanol. Collections were made with permits provided by ICMBio (Instituto Chico Mendes de Conservação da Biodiversidade) and field methods have been approved by CEUA-CCS-UFRJ (Ethics Committee for Animal Use of Federal University of Rio de Janeiro; permit number: 01200.001568/2013-87). Material is deposited in Instituto de Biologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro (UFRJ) and Coleção Ictiológica do Centro de Ciências Agrárias e Ambientais, Universidade Federal do Maranhão, Chapadinha (CICCAA). Descriptions of colouration of living fish were based on observations just after collections, in small transparent plastic bottles. Type specimens were photographed live about 24 hours after collection. Measurements and counts follow Costa (1988). Measurements are presented as percentages of standard length (SL), except for those related to head morphology, which are expressed as percentages of head length. Fin-ray counts include all elements. Osteological preparations followed Taylor and Van Dyke (1985); the abbreviation C&S in lists of material indicates those specimens that were cleared and stained for osteological examination. Terminology for osteological structures followed Costa (2006), for frontal squamation Hoedeman (1958), and for cephalic neuromast series Costa (2001). In lists of material, geographical features are written according to Brazilian Portuguese local use (e.g., córrego, ribeirão, rio), allowing more accurate identifications of localities in the field and avoiding common mistakes when tentatively translating them to English.

Results

Melanorivulus proximus sp. n.

http://zoobank.org/79A16259-1DEF-4F9E-8AE1-047802792F3F

Figs 1–2, Table 1

Rivulus pictus (non *Rivulus pictus* Costa, 1989); Costa 1995: 216 (misidentification).

Rivulus scalaris (non *Rivulus scalaris* Costa, 2005); Costa 2005: 79 (misidentification).

Holotype. UFRJ 11681, male, 27.7 mm SL; Brazil: Mato Grosso do Sul state: Cassilândia municipality: stream crossing the road MS-306, Rio Aporé drainage, Rio Paraná Basin, 19°03'54"S, 51°49'56"W, altitude about 515 m asl; W.J.E.M. Costa et al., 20 Sep. 2011.

Paratypes. All from Brazil: Rio Aporé drainage, upper Rio Paraná Basin. Mato Grosso do Sul state: UFRJ 10792, 4 males, 25.6–30.0 mm SL, 1 female, 25.6 mm SL; UFRJ 10793, 1 male, 23.6 mm SL, 1 female, 21.1 mm SL (C&S); collected with holotype. – UFRJ 10788, 6 males, 15.7–27.7 mm SL, 4 females, 24.0–27.4 mm SL; UFRJ 10789, 3 males, 20.9–21.9 mm SL, 2 females, 18.5–20.0 mm SL (C&S); CICCAA 00692, 5 males, 21.9–25.8 mm SL, 5 females, 21.7–25.6 mm SL; Cassilândia municipality: road MS-306, 19°02'15"S, 52°01'57"W, altitude about 540 m asl; W.J.E.M. Costa et al., 20 Sep. 2011.– UFRJ 2207, 8 males, 20.2–27.1 mm SL, 12 females, 17.8–35.4 mm SL.; UFRJ 2280, 1 male, 25.9 mm SL, 2 females, 27.9–28.7 mm SL (C&S); Cassilândia municipality: swamp close to Ribeirão Grande, road MS-306, about 30 km SE from the town of Cassilândia, 19°15'40"S, 51°30'03"W, altitude about 495 m asl; W.J.E.M. Costa et al., 17 Sep. 1994. Goiás state: UFRJ 10821, 1 male, 27.7 mm SL, 1 female, 22.7 mm SL; UFRJ 10822, 4 males, 15.6–18.4 mm SL, 12 females, 16.2–22.1 mm SL; Itajá municipality: Ribeirão Bagageiro, road GO-302, 19°06'17"S, 51°42'15"W, altitude about 455 m asl; W.J.E.M. Costa, B.B. Costa & C.P. Bove, 15 Jan. 2007.

Additional material (non-types). UFRJ 10819, 12; Brazil: Goiás state: Itajá municipality: road GO-302, 19°05'09"S, 51°36'27"W, altitude about 440 m asl; W.J.E.M. Costa et al., 20 Sep. 2011.

Figure 1. *Melanorivulus proximus* sp. n., holotype, UFRJ 11681, male, 27.7 mm SL. Photograph by W.J.E.M. Costa.

Figure 2. *Melanorivulus proximus* sp. n., paratype, UFRJ 10792, female, 26.6 mm SL. Photograph by W.J.E.M. Costa.

Diagnosis. *Melanorivulus proximus* is distinguished from all other congeners of the *M. pictus* group except *M. scalaris* by the presence of irregularly arranged, interconnected oblique red bars on flank, forming Y- and X-shaped marks. *Melanorivulus proximus* is distinguished from *M. scalaris* by: caudal fin base colour pale orangish pink in females (vs. pale yellow); dorsal and anal fin sharply pointed in males (vs. rounded to moderately pointed), dorsal-fin origin at vertical between base of 9th and 10th (vs. between base of 7th and 8th); longitudinal series of scales 29–30 (vs. 31–34); pre-dorsal length longer in males (75.9–78.4 % SL vs. 73.0–75.0 % SL); longer anal-fin base (21.1–24.7 % SL in males and 18.8–21.4 % SL in females vs. 18.1–21.0 % SL in males and 16.2–18.5 % SL in females); and fewer infraorbital neuromasts around orbit (9–10 vs. 11–12).

Description. Morphometric data appear in Table 1. Body relatively deep, subcylindrical anteriorly, slightly deeper than wide, compressed posteriorly. Greatest body depth at vertical just anterior to pelvic-fin base. Dorsal and ventral profiles of trunk slightly convex in lateral view, approximately straight on caudal peduncle. Head moderately wide, sub-triangular in lateral view, dorsal profile nearly straight, ventral profile convex. Snout blunt. Jaws short; teeth numerous, conical, irregularly arranged; outer teeth hypertrophied, inner teeth small and numerous. Vomerine teeth 3–5. Gill-rakers on first branchial arch 2 + 7–8.

Dorsal and anal fins short, sharply pointed in males, rounded to slightly pointed in females. Caudal fin rounded, slightly longer than deep. Pectoral fin rounded, posterior margin reaching vertical at about 90 % of length between pectoral-fin and pelvic-fin bases. Pelvic fin small, longer in males, tip reaching between base of 2nd and 3rd anal-fin rays in males, reaching anus in females; pelvic-fin bases medially in close proximity. Dorsal-fin origin at vertical between base of 9th and 10th anal-fin rays. Dorsal-fin rays 9–11; anal-fin rays 13–15; caudal-fin rays 30–32; pectoral-fin rays 13–14; pelvic-fin rays 7. No contact organs on fins. Second proximal radial of dorsal

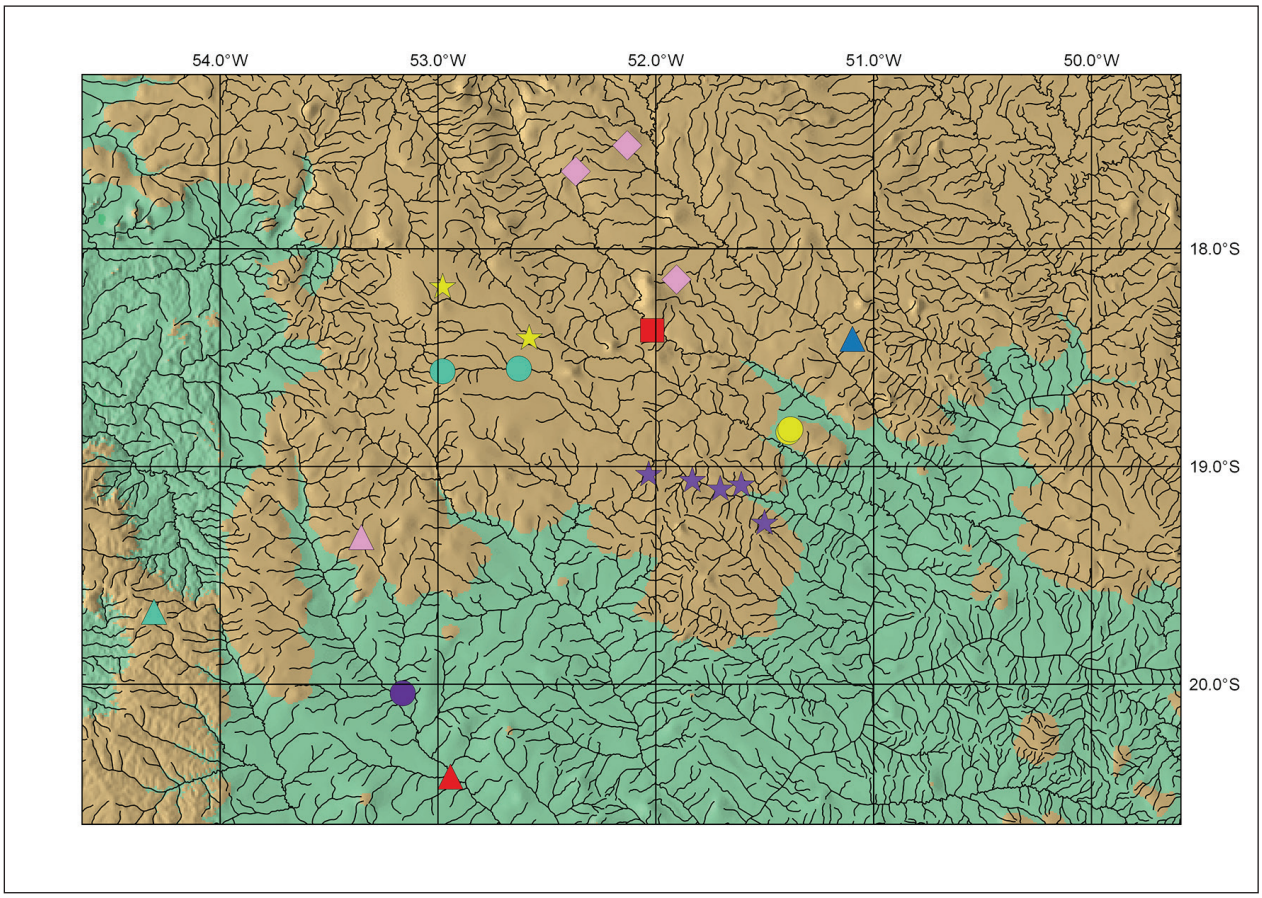

Figure 3. Geographical distribution of killifishes of the *Melanorivulus pictus* species group in the rivers draining the south-eastern slope of the Caiapó range and the adjacent middle Rio Paraná Basin. Blue triangle: *M. vittatus*; light green dot: *M. scalaris*; light green triangle: *M. linearis*; pink lozenges: *M. faucireticulatus*; pink triangle: *M. egens*; purple dot: *M. nigropunctatus*; purple stars: *M. proximus*; red square: *M. rutilicaudus*; red triangle: *M. ofaie*; yellow dots: *M. nigromarginatus*; yellow stars: *M. formosensis*.

fin between neural spines of 18th and 20th vertebrae; first proximal radial of anal fin between pleural ribs of 13th and 14th vertebrae; total vertebrae 30–31.

Scales small, cycloid. Body and head entirely scaled, except anterior ventral surface of head. Body squamation extending over anterior 25 % of caudal-fin base; no scales on dorsal, anal and pectoral-fin bases. Frontal squamation E-patterned; E-scales not overlapping medially; scales arranged in regular circular pattern around A-scale without exposed margins; transverse row of scales anterior to H-scale. Five supraorbital scales. Longitudinal series of scales 29–30; transverse series of scales 8; scale rows around caudal peduncle 16. No contact organs on scales. Cephalic neuromasts: supraorbital 3 + 3, parietal 1, anterior rostral 1, posterior rostral 1, infraorbital 1 + 9–10 + 1, preorbital 2, otic 1, post-otic 2, supratemporal 1, median opercular 1, ventral opercular 1, preopercular 2 + 4, mandibular 3 + 1, lateral mandibular 2–3, paramandibular 1. Lateral line interrupted, alternating sets of 3–4 scales with one neuromast and without neuromasts. Two neuromasts on caudal-fin base.

Colouration in life. ***Males.*** Flank metallic greenish blue to bright blue, with narrow oblique red bars between humeral region and posterior portion of caudal peduncle; bars irregularly arranged, forming chevron-like marks with angle varying in position on flank, often connected to short adjacent bars, forming Y- and X-shaped marks; bars with minute vertical extensions on each scale margin; dorsal portion of flank with oblique rows of red dots; anteroventral portion of flank with rows of red dots, often coalesced to form zigzag red marks. Dorsolateral portion of body, between posterior part of head and anterior part of flank, above humeral region, pale golden. Humeral region with horizontally elongated black spot. Dorsum light brown, venter white. Opercular region greenish golden with dark red reticulation on scale margins; suborbital region yellowish white; lower jaw dark grey. Iris pale yellow, with dark brown bar on anterior and posterior portions. Dorsal fin bluish white, sometimes yellowish on distal portion, with 4–5 transverse, narrow faint red or red stripes. Anal fin pale yellow, base and posterior portion bluish white with row of light red dots or short stripes. Caudal fin pale yellow to bluish white, with 5–6 narrow red or reddish orange stripes. Pectoral fin yellowish hyaline. Pelvic fin orangish pale yellow.

Females. Similar to males, except flank base colour pale greenish golden; dorsal and caudal fin bars dark grey; caudal fin base colour pale orangish pink; and pres-

Table 1. Morphometric data of *Melanorivulus proximus*.

Measurements	Holotype	Paratypes	
	male	males (7)	females (5)
Standard length (mm)	27.7	25.6–30.0	24.0–27.4
Percent of standard length			
Body depth	25.6	22.6–25.0	22.8–23.5
Caudal peduncle depth	15.1	14.1–14.9	13.1–14.2
Pre-dorsal length	78.4	75.9–78.3	76.1–79.7
Pre-pelvic length	57.1	54.7–56.5	55.0–57.9
Length of dorsal-fin base	11.2	10.4–12.8	10.7–12.9
Length of anal-fin base	22.2	21.1–24.7	18.8–21.4
Caudal-fin length	36.9	33.7–39.8	31.6–36.8
Pectoral-fin length	22.8	19.9–22.3	18.9–22.8
Pelvic-fin length	12.4	12.0–13.4	9.1–9.6
Head length	29.3	27.0–29.2	26.9–29.3
Percent of head length			
Head depth	72.0	68.6–72.8	69.3–73.0
Head width	71.1	70.5–73.4	72.7–76.0
Snout length	13.5	13.6–15.2	14.5–16.8
Lower jaw length	18.4	19.9–22.0	19.7–21.8
Eye diameter	33.2	30.3–34.6	30.2–35.7

ence of black spot on dorsal portion of caudal-fin base and dark grey pigmentation concentrated on distal margins of dorsal and anal fins, anterior margin of pelvic fin and entire caudal-fin margin.

Colouration in alcohol. Head and trunk pale brown, fins whitish hyaline; dark marks recorded for live specimens varying from dark brown to black.

Distribution. Middle section of the Rio Aporé drainage, upper Rio Paraná Basin, central Brazil (Fig. 3).

Etymology. From the Latin *proximus* (near, neighbour), referring to its distribution area at the same drainage as *M. scalaris*.

Melanorivulus nigromarginatus sp. n.

http://zoobank.org/FC9E4B2E-47F2-46E4-B779-67CB5B81E667
Figs 4–5, Table 2

Holotype. UFRJ 8434, male, 27.6 mm SL; Brazil: Goiás state: Itarumã municipality: Córrego Lajeado, Rio Corrente drainage, upper Rio Paraná Basin, road GO-178, 18°49'45"S, 51°22'55"W, altitude about 470 m asl; W. J. E. M. Costa et al., 20 Sep. 2011.

Paratypes. Brazil: Estado de Goiás: Município de Itarumã: all from the Corrente River drainage, upper Paraná River Basin. UFRJ 8436, 5 males, 23.4–24.7 mm SL, 8 females, 23.0–27.7 mm SL; CICCAA 00693, 5 males, 19.4–23.5 mm SL, 5 females, 20.4–24.0 mm SL; UFRJ 8435, 1 male, 23.3 mm SL, 5 females, 22.5–25.4 mm SL (C&S); collected with holotype. – UFRJ 8440, 11 males, 25.4–35.6 mm SL, 7 females, 24.7–30.8 mm SL; UFRJ 8442, 4 males, 27.6–32.9 mm SL, 2 females, 26.6–27.9 mm SL (C&S); Córrego Barreiro, road GO-178, 18°50'30"S, 51°23'27"W, altitude 498 m; W.J.E.M. Costa et al., 15 Jan. 2007. – UFRJ 8439, 2 males, 27.0–30.0 mm SL, 1 female, 25.1 mm SL; same locality as UFRJ 8440; W.J.E.M. Costa et al., 20 Sep. 2011.

Diagnosis. *Melanorivulus nigromarginatus* is similar to *M. egens* and *M. linearis*, and distinguished from all other species of the *M. pictus* group by the presence of a black distal marginal stripe on the anal fin in males (vs. absence). *Melanorivulus nigromarginatus* is distinguished from *M. egens* and *M. linearis* by having melanophores strongly concentrated on the post-orbital and humeral regions, forming a stripe (vs. weakly concentrated, not forming distinct marks); presence of red dots on the anteroventral portion of flank (vs. absence); presence of red bars on most portion of caudal fin in males (vs. bars absent in *M. egens* and bars restricted to the dorsal portion of the caudal fin in *M. linearis*); and red chevron-shaped marks irregularly distributed on the flank (vs. regularly). In addition, although not useful to distinguish all specimens, *M. nigromarginatus* often have more scales in the longitudinal series than *M. egens* and *M. linearis* (31–33 vs. 29–31).

Description. Morphometric data appear in Table 2. Body relatively deep, sub-cylindrical anteriorly, deeper than wide, compressed posteriorly. Greatest body depth at vertical just anterior to pelvic-fin base. Dorsal and ventral profiles of trunk slightly convex in lateral view; dorsal and ventral profiles of caudal peduncle nearly straight. Head moderately wide, sub-triangular in lateral view, dorsal profile nearly straight, ventral profile convex. Snout blunt. Jaws short; teeth numerous, conical, irregularly arranged; outer teeth hypertrophied, inner teeth small and numerous. Vomerine teeth 2–5. Gill-rakers on first branchial arch 1 + 8.

Dorsal and anal fins short, tip slightly pointed in males, rounded in females. Caudal fin rounded, slightly longer than deep. Pectoral fin rounded, posterior margin reaching vertical just anterior to pelvic-fin insertion. Pelvic fin small, longer in males, tip reaching between urogenital papilla and base of 2nd anal-fin ray in male, reaching anus in females; pelvic-fin bases medially in close proximity. Dorsal-fin origin at vertical between base of 8th and 9th anal-fin rays. Dorsal-fin rays 10–11; anal-fin rays 13–15; caudal-fin rays 31–34; pectoral-fin rays 13; pelvic-fin rays 6–7. No contact organs on fins. Second proximal radial of dorsal fin between neural spines of 19th and 21st vertebrae; first proximal radial of anal fin between pleural ribs of 13th and 15th vertebrae; total vertebrae 30–32.

Scales small, cycloid. Body and head entirely scaled, except anterior ventral surface of head. Body squamation extending over anterior 25 % 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 30–33;

Figure 4. *Melanorivulus nigromarginatus* sp. n., holotype, UFRJ 8434, male, 27.6 mm SL. Photograph by W.J.E.M. Costa.

Figure 5. *Melanorivulus nigromarginatus* sp. n., paratype, UFRJ 8436, female, 23.8 mm SL. Photograph by W.J.E.M. Costa.

Table 2. Morphometric data of *Melanorivulus nigromarginatus*.

Measurements	Holotype	Paratypes	
	male	males (10)	females (8)
Standard length (mm)	27.6	25.4–35.6	24.7–30.8
Percent of standard length			
Body depth	22.4	23.4–24.7	22.1–24.6
Caudal peduncle depth	14.4	14.2–15.5	13.1–15.0
Pre-dorsal length	74.4	73.7–77.4	76.6–78.5
Pre-pelvic length	55.5	53.9–56.4	56.4–58.8
Length of dorsal-fin base	13.9	12.5–15.7	11.2–13.2
Length of anal-fin base	22.8	21.1–25.0	18.1–21.6
Caudal-fin length	36.6	33.0–38.3	32.7–36.9
Pectoral-fin length	20.6	20.5–23.2	20.4–22.6
Pelvic-fin length	12.3	12.2–15.2	9.4–10.4
Head length	27.0	26.2–27.5	26.8–28.5
Percent of head length			
Head depth	67.8	67.2–73.8	68.6–74.8
Head width	74.4	73.4–77.6	75.6–81.0
Snout length	14.7	13.4–15.5	12.6–15.2
Lower jaw length	20.6	18.1–22.2	16.5–20.8
Eye diameter	32.7	30.6–33.2	29.8–33.0

transverse series of scales 9; scale rows around caudal peduncle 16. No contact organs on scales. Cephalic neuromasts: supraorbital 3 + 3, parietal 1, anterior rostral 1, posterior rostral 1, infraorbital 1 + 10–12 + 1, preorbital 2, otic 1, post-otic 1, supratemporal 1, median opercular 1, ventral opercular 1, pre-opercular 2 + 4, mandibular 3 + 1, lateral mandibular 1–2, paramandibular 1.

Colouration. ***Males***. Flank metallic light green, with narrow oblique red bars between humeral region and posterior portion of caudal peduncle; bars irregularly arranged, forming chevron pattern directed anteriorly, usually fragmented, with angle on flank midline or above it; bars with minute vertical extensions on each scale margin; dorsal portion of flank with oblique rows of red dots; anteroventral portion of flank with rows of red dots. Dorsum light brown, venter white. Side of head light brown on dorsal portion, yellowish white on ventral portion to pale golden on opercle; broad dark grey to black postorbital stripe, continuous to humeral black blotch; lower jaw dark grey. Iris pale yellow, with dark brown bar on anterior and posterior portions. Dorsal fin light yellow, with four to six oblique faint red bars. Anal fin light yellow to orange, basal portion greenish white with five or six orangish red spots, distal margin black. Caudal fin light yellow, with six to eight narrow orangish red bars extending on entire caudal fin, except its ventral-most portion. Pectoral fin hyaline. Pelvic fin light yellow to orange narrow black margin.

Females. Similar to males, except flank base colour pale greenish blue; dorsal and caudal fin bars dark grey;

caudal fin base colour pale orangish pink; absence of black pigmentation on post-orbital and humeral regions; and presence of black spot on dorsal portion of caudal-fin base and dark grey pigmentation concentrated on distal margins of dorsal and anal fins, anterior margin of pelvic fin and entire caudal-fin margin.

Colouration in alcohol. Head and trunk pale brown, fins whitish hyaline; dark marks recorded for live specimens varying from dark brown to black.

Distribution and conservation. Known only from two close small streams in the middle section of the Corrente River drainage, upper Paraná River Basin (Fig. 3).

Etymology. The name *nigromarginatus* (black margin), from the Latin, is a reference to the presence of a black margin on the anal in males.

Melanorivulus linearis sp. n.

http://zoobank.org/9312393A-94FD-4433-9818-88CC6F1666D9
Figs 6–7, Table 3

Holotype. UFRJ 11678, male, 25.1 mm SL; Brazil: Mato Grosso do Sul state: Bandeirantes municipality: Córrego Água Limpa, upper Rio Pardo drainage, Rio Paraná basin, 19°40'01"S, 54°18'13"W, altitude about 620 m asl; W.J.E.M. Costa, B.B. Costa & C.P. Bove, 12 Jan. 2004.

Paratypes. UFRJ 11679, 2 males, 27.9–30.1 mm SL, 7 females, 15.8–23.7 mm SL; UFRJ 11680, 2 males, 20.8–26.0 mm SL, 2 females, 19.5–21.1 mm SL (C&S); CICCAA 00694, 2 males, 19.0–27.2 mm SL, 3 females, 19.6–20.5 mm SL; collected with holotype.

Diagnosis. *Melanorivulus linearis* is similar to *M. egens*, and distinguished from all other species of the *M. pictus* group by the presence of red chevron-shaped marks regularly distributed on the flank (vs. irregularly), absence of distinctive dark marks on humeral region (vs. presence), and absence of red dots on the anteroventral portion of flank (vs. presence). *Melanorivulus linearis* is distinguished from *M. egens* by the presence of red bars restricted to the dorsal portion of the caudal fin in males (vs. absence), presence of black bars on the caudal fin in females (vs. black dots); presence of a pale green spot on humeral region in males (vs. absence); and second proximal radial of the dorsal fin between neural spines of 18th and 19th vertebrae (vs. between neural spines of 19th and 21st vertebrae).

Description. Morphometric data appear in Table 3. Body relatively deep, sub-cylindrical anteriorly, deeper than wide, compressed posteriorly. Greatest body depth at vertical just anterior to pelvic-fin base. Dorsal and ventral profiles of trunk slightly convex in lateral view; dorsal and ventral profiles of caudal peduncle nearly straight. Head moderately wide, sub-triangular in lateral view, dorsal profile nearly straight, ventral profile convex. Snout blunt. Jaws short; teeth numerous, conical, irregularly arranged; outer teeth hypertrophied, inner teeth small and numerous. Vomerine teeth 3–5. Gill-rakers on first branchial arch 1 + 8.

Dorsal and anal fins short, tip slightly pointed in males, rounded in females. Caudal fin rounded, slightly longer than deep. Pectoral fin rounded, posterior margin reaching vertical just anterior to pelvic-fin insertion. Pelvic fin small, longer in males, tip reaching between base of 2nd or 3rd anal-fin ray in males, reaching between anus and urogenital papilla in females; pelvic-fin bases medially in close proximity. Dorsal-fin origin on vertical through base of 8th or 9th anal-fin ray. Dorsal-fin rays 10–11; anal-fin rays 13–15; caudal-fin rays 31–32; pectoral-fin rays 13–14; pelvic-fin rays 7. No contact organs on fins. Second proximal radial of dorsal fin between neural spines of 18th and 19th vertebrae; first proximal radial of anal fin between pleural ribs of 13th and 15th vertebrae; total vertebrae 30–31.

Scales small, cycloid. Body and head entirely scaled, except anterior ventral surface of head. Body squamation extending over anterior 25 % 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 29–31; transverse series of scales 9; scale rows around caudal peduncle 16. No contact organs on scales. Cephalic neuromasts: supraorbital 3 + 3, parietal 1, anterior rostral 1, posterior rostral 1, infraorbital 1 + 9–11 + 1, preorbital 2, otic 1, post-otic 1–2, supratemporal 1, median opercular 1, ventral opercular 1, pre-opercular 2 + 4, mandibular 3 + 1, lateral mandibular 1–2, paramandibular 1.

Colouration. ***Males***. Flank metallic greenish blue, sometimes purplish blue above anal fin, with oblique narrow red bars between humeral region and posterior portion of caudal peduncle; bars regularly arranged, forming chevron pattern directed anteriorly, with angle on flank midline or above it; bars with minute vertical extensions on each scale margin; dorsal portion of flank with few red dots; anteroventral portion of flank without red marks; pale green spot on humeral region. Dorsum light brown, venter white. Side of head light brown on dorsal portion, yellowish white on ventral portion to pale golden on opercle; melanophores dispersed, not forming distinct marks on post-orbital region; lower jaw dark grey. Iris pale yellow, sometimes with dark brown bar on anterior and posterior portions. Dorsal fin light yellow, with four to six oblique red bars through whole fin. Anal fin yellowish orange, basal portion purplish white with six or seven short red bars, distal margin black. Caudal fin light yellow, with six to eight narrow red bars extending between dorsal and middle portions of fin; fin margin dark grey. Pectoral fin hyaline. Pelvic fin light yellow with narrow black margin.

Figure 6. *Melanorivulus linearis* sp. n., holotype, UFRJ 11678, male, 25.1 mm SL. Photograph by W.J.E.M. Costa.

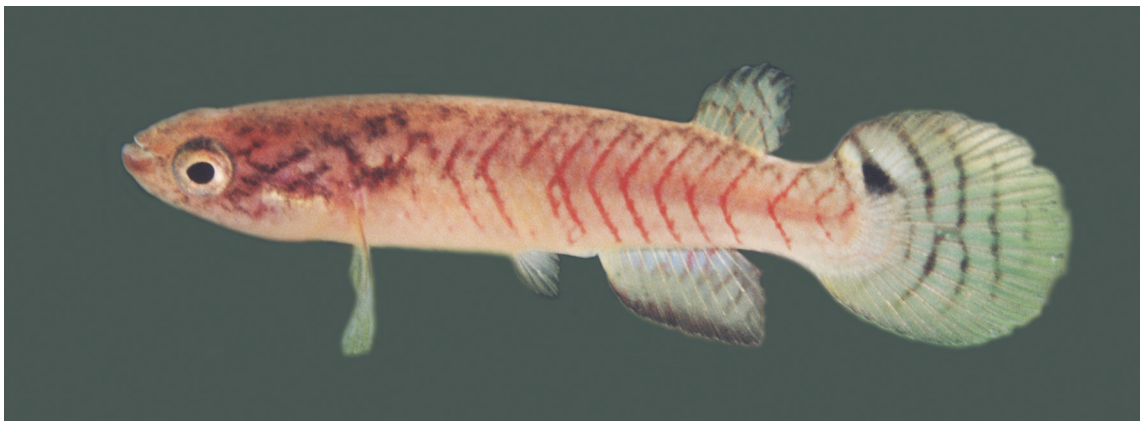

Figure 7. *Melanorivulus linearis* sp. n., paratype, UFRJ 11679, 23.4 mm SL. Photograph by W.J.E.M. Costa.

Table 3. Morphometric data of *Melanorivulus linearis*.

Measurements	Holotype	Paratypes	
	male	males (4)	females (5)
Standard length (mm)	25.1	27.2–30.1	20.7–23.7
Percent of standard length			
Body depth	25.1	23.4–25.1	22.3–23.1
Caudal peduncle depth	15.9	14.4–16.2	12.9–14.1
Pre-dorsal length	75.3	75.4–77.4	77.1–78.7
Pre-pelvic length	57.2	54.6–55.8	54.2–58.0
Length of dorsal-fin base	12.6	12.0–12.8	10.5–12.8
Length of anal-fin base	22.2	19.3–21.6	17.9–19.0
Caudal-fin length	36.8	34.6–36.9	34.2–37.4
Pectoral-fin length	20.8	20.8–21.7	20.8–22.4
Pelvic-fin length	14.8	13.1–15.4	8.6–9.3
Head length	28.2	26.7–29.3	27.8–28.8
Percent of head length			
Head depth	73.1	69.6–72.4	67.7–71.7
Head width	69.7	72.5–74.9	70.5–74.0
Snout length	13.4	12.7–14.8	12.4–14.1
Lower jaw length	15.0	16.2–19.3	16.2–19.5
Eye diameter	32.0	29.7–31.1	32.8–35.3

Females. Similar to males, except flank base colour pale greenish golden; no distinct marks on humeral region; dorsal and caudal fin bars dark grey to black; caudal fin base colour pale white; absence of pale green spot on humeral region; and presence of triangular black spot on dorsal portion of caudal-fin base and dark grey pigmentation concentrated on distal margins of dorsal and anal fins, anterior margin of pelvic fin and entire caudal-fin margin.

Distribution. Known only from the type locality, upper section of the Rio Pardo, middle Rio Paraná Basin, central Brazil (Fig. 3).

Etymology. From the Latin, *linearis* (consisting of lines), an allusion to the red oblique lines regularly arranged on the flank in males.

Discussion

Studies on systematics of *Melanorivulus* have consistently demonstrated the importance of colour pattern characters both to diagnose species and to support monophyletic groups (Costa 2016). According to recent phylogenetic analyses (Costa 2016; Costa et al. 2016), colour pattern characters highly corroborates groups that are supported by other morphological characters, as well as by molecular data. However, the relatively low variability of mor-

Figure 8. *Melanorivulus scalaris*, UFRJ 6494, male, 29.7 mm SL. Photograph by W.J.E.M. Costa.

phometric, meristic and osteological characters among species of the *M. pictus* group makes colour pattern characters essential source to diagnose species and to estimate their relationships, since molecular data are not still available for most species. Consequently, the new taxa herein described exhibit colour patterns characters that in combination easily allow their recognition as new species, but their relationships are still unclear.

Melanorivulus proximus is the second species recorded for the Rio Aporé drainage. *Melanorivulus scalaris* also occurs in the Aporé drainage, but in altitudes between about 740 and 800 m asl, whereas *M. proximus* is here reported for altitudes between about 440 and 540 m asl. The veredas of this drainage were first sampled in 1994, but specimens here recognised as belonging to *M. proximus* were then identified as *M. pictus* (Costa, 1995; see Introduction above for historical context). Costa (2005) described *Rivulus scalaris* Costa, 2005 (= *M. scalaris*) based on material collected in the Ribeirão São Luiz, upper Rio Sucuruí drainage. Specimens collected in the middle section of the Rio Aporé drainage were then tentatively identified as *M. scalaris* and listed as additional material (non-types). Costa (2007) recorded *R. scalaris* to the Rio da Prata floodplains, upper Rio Aporé drainage, in a plateau area where the upper Ribeirão São Luiz and the Rio da Prata are in contact. However, the taxonomic status of the middle Aporé populations was not clarified until now.

The frequent occurrence of irregularly interconnected chevron-shaped red marks on the flank in males of *M. proximus* suggests that it is closely related to *M. scalaris*, in which this colour pattern is always present (Fig. 8). However, the pointed anal fin in males and the strongly pigmented reticulation on the head side in females, suggest that *M. proximus* is more closely related to species endemic to neighbouring drainages that exhibit these derived character states, comprising *M. faucireticulatus* from the Claro and Verde river drainages (Costa 2007b: figs 1–2) and *M. rutilicaudus* from the Rio Verde drainage (Costa 2005: Figs 8–9). In large adult specimens of *M. scalaris* the anal fin tip is not pointed (Fig. 8) and the caudal fin is pale yellow in females (Fig. 9).

Previous studies indicate that the Sucuruí, Aporé, Corrente, Verde and Claro river drainages, which drain the south-eastern slope of the Caiapó range and flow directly to the Rio Paranaíba as part of the upper Rio Paraná Basin, concentrates a great diversity of species of *Melanorivulus* (Costa 2005, 2007a, b, 2008). These species are often members of clades endemic to Caiapó range drainages, including those belonging to the upper Rio Araguaia Basin, on its northern slope (e.g., Costa 2006). However, characters supporting phylogenetic relationships of *M. nigromarginatus*, from the Rio Corrente drainage, with other species of the Caiapó range drainages are ambiguous.

Melanorivulus nigromarginatus is easily distinguished from all other species endemic to the Caiapó range drainages by the presence of a black marginal band on the anal fin in males (Fig. 4), suggesting that it may be more closely related to *M. egens* (Costa 2005: fig. 11) and *M. linearis* (Fig. 6), which also have similar black anal-fin margin, but are endemic to tributaries of the middle section of the Rio Paraná (Fig. 3). Contrastingly, the presence of a distinctive dark humeral spot in *M. nigromarginatus* suggests that it may be more closely related to other species occurring in other Caiapó range drainages (e.g., *M. faucireticulatus*, *M. formosensis*, *M. proximus*, *M. rutilicaudus*, *M. scalaris*, *M. vittatus*). All these species share the presence of a distinct humeral blotch varying from dark red to black (Figs 1–2, 4–5), whereas this derived condition is not present in *M. egens* and *M. linearis* (Figs 6–7). In addition, the presence of orangish pink pigmentation on the caudal fin in females that occur in *M. nigromarginatus* (Fig. 5), *M. proximus* (Fig. 2), *M. faucireticulatus* (Costa 2007b: fig. 2), and *M. rutilicaudus* (Costa 2005: fig. 9), reinforces the hypothesis of close relationships. On the other hand, probably *M. egens* and *M. linearis* from the middle Rio Paraná Basin are closely related species, sharing the presence of red chevron-shaped

Figure 9. *Melanorivulus scalaris*, UFRJ 6494, female, 24.2 mm SL. Photograph by W.J.E.M. Costa.

marks regularly distributed on the flank in males (Fig. 6; Costa 2005: fig. 11).

The present study once more reports the occurrence of different species of *Melanorivulus* inhabiting separate sections of the same river drainage as already described in previous studies (Costa 2007b, 2017; Volcan et al. 2017; Fig. 3). Recently, Costa (2017) compared this distributional pattern to that reported for other vertebrates occurring in the Cerrado, which is explained to be correlated with Miocene topographical reorganization causing geographical isolation of ancestral populations in plateaus and peripheral depressions (Prado et al. 2012; Guarnizo et al. 2016). Although estimates of divergence time among lineages of the *M. pictus* group are not still available, this paleogeographical scenario could explain the present distribution of distinct species of *Melanorivulus* at different altitudinal zones of river drainages.

Costa (2012) reported a strong process of habitat loss in the rivers draining the Caiapó range as a result of the quick expansion of agriculture land use in areas previously occupied by natural vegetation. In recent years, the veredas have often been extirpated after diversion of their water sources for plantation irrigation, as well as widespread deforestation, which has reached their margins when water flow persists. Considering the great diversity of endemic species of *Melanorivulus* inhabiting the Veredas of the Caiapó range and the continuous extirpation of Vereda habitats, this study supports the endangered status of species inhabiting this region.

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