

Copyright © 2013 Magnolia Press





http://dx.doi.org/10.11646/zootaxa.3641.2.3

http://zoobank.org/urn:lsid:zoobank.org:pub:CD620174-4898-4F8C-9200-E6D5CD9E7A9C

Crenicichla gillmorlisi, a new species of cichlid fish (Teleostei: Cichlidae) from the Paraná river drainage in Paraguay

SVEN O. KULLANDER¹ & CARLOS A. SANTOS DE LUCENA²

¹Department of Zoology, Swedish Museum of Natural History, POB 50007, SE-104 05 Stockholm, Sweden. E-mail: sven.kullander@nrm.se ²Laboratório de Ictiologia, Museu de Ciências e Tecnologia da PUCRS, Caixa Postal 1429, 90620 Porto Alegre, Rio Grande do Sul, Brazil. E-mail:lucena@pucrs.br

Abstract

Crenicichla gillmorlisi, new species, is described from the río Acaray, a right bank tributary to the río Paraná. It is most similar to *C. mandelburgeri* in proportional measurements and meristics, but differs in colour pattern, adults having the body covered with small spots.

Key words: Endemism, freshwater, South America, taxonomy

Resúmen

Se describe *Crenicichla gillmorlisi*, nueva especie, del río Acaray, un afluente del lado derecho del río Paraná. Es más parecido al *C. mandelburgeri* en medidas proporcionales y meristicas, distinguido por su padrón de colorido, con el cuerpo y las aletas dorsal, anal y caudal cubiertos por pequeñas manchas.

Introduction

The South American cichlid genus *Crenicichla* Heckel is the most speciose genus of the family Cichlidae, with close to 85 valid species (Kullander 2003; Casciotta *et al.* 2006b; Kullander & Lucena 2006; Piálek *et al.* 2010; Varella *et al.* 2012). Whereas South American cichlid species diversity is highest in the Amazon basin, recent studies have demonstrated a proportionally high number of species of *Crenicichla* in southern and southeastern South America. Lucena & Kullander (1992) reported on 11 species from the río Uruguay basin, of which nine endemic, to which Lucena (2007) added two species, also endemic. Kullander & Lucena (2006) distinguished six species, of which three new, from the coastal rivers of Brazil and eastern Uruguay. Ten endemic species are described from the río Paraná drainage (Casciotta *et al.* 2010; Kullander 2003, 2009; Piálek *et al.*, 2010), and additional species are suggested by the molecular analysis by Piálek *et al.* (2012)

Six species of *Crenicichla* have been reported from Paraguay (Kullander 2003, 2009). *Crenicichla vittata* Heckel is relatively widespread in the Paraguay and lower Paraná basins and the río Uruguay. *Crenicichla lepidota* Heckel occurs in the Guaporé and Paraguay basins, and also in the middle and lower Paraná basin, the Uruguay basin, coastal rivers in Uruguay and in the Laguna dos Patos basin in Brazil. *Crenicichla semifasciata* (Heckel) is mainly distributed in the río Paraguay drainage, but occurs also in the adjacent lower Paraná. *Crenicichla mandelburgeri* Kullander was described recently from the rivers Poromoco, Pirayuy, Pirapó and Tembey, which are right bank tributaries to the río Paraná (Kullander 2009), and it was subsequently reported by Piálek *et al.* (2012) from Argentinian tributaries from Guaruhapé north to río Urugua-í. Piálek *et al.* (2012) also recognized a species similar to *C. mandelburgeri* from slightly more downstream localities in both Argentina and Paraguay. Kullander (1981) reported one more species from both the Brazilian and the Paraguayan side of the Paraná, within the Itaipú dam, tentatively identified as *C. niederleinii* (Holmberg).

The present paper reports on samples of *Crenicichla* made from 1980 onward, representing a new species apparently restricted to the río Acaray, a right bank tributary of the río Paraná with its mouth immediately downstream of the Itaipú reservoir.

Materials and methods

Measurements and counts were taken as described by Kullander (1986). Specimen lengths are given as standard length (SL), measured from the tip of the upper jaw to the middle of the base of the caudal fin. Scales in a longitudinal row (E1 row scales) are counted in the row immediately dorsal to that containing the lower lateral line. Colour marking terminology follows Kullander (1986). Vertebral counts include the last halfcentrum and were taken from X-radiographs made on Kodak X-omat V film using a Philips MG-105 low voltage X-ray unit. Morphometric data were managed and analysed using IBM SPSS Statistics, ver. 20 (IBM 2011), and SMATR (Falster *et al.* 2006). Paraguayan toponyms vary with regard to the final i (Guarani word for water or small) in names of rivers and streams. Acaray could also be written Acaraí, Acara'i or Acara-i. We chose here the more common -y ending.

Specimens are deposited in the following institutions: MNHNP, Museo Nacional de Historia Natural del Paraguay, San Lorenzo; MHNG, Muséum d'Histoire naturelle de Genève, Geneva; MHNIB, Colección de Referencia, Itaipú Binacional, Ciudad del Este; NRM, Swedish Museum of Natural History, Stockholm;

Kullander (1981) reported on a species of *Crenicichla* from near Guairá and Itaipú, provisionally identified as *C. niederleinii*. This identification still must rate as provisional, and we here prefer to adopt the appellation *Crenicichla* "PARANÁ", suggested to us by Henrique Varella (pers. comm.), who is conducting a revision of species of *Crenicichla* in the Paraná basin. Species groups of *Crenicichla* are those recognized by Kullander *et al.* (2010).

Comparative material is as listed in Kullander (2009), and Kullander & Lucena (2006), with the addition of:

Crenicichla semifasciata, Paraguay, río Paraguay drainage: NRM 43342. 1, 55.8 mm SL. Concepción, río Paraguay right side shore at Estancia La Novia. 20 Apr 1999. E. Åhlander *et al.*—NRM 44582. 1, 171.2 mm SL. San Pedro, río Paraguay, left shore about 11 km downstream of Antequera. 22 Apr 1999. E. Åhlander *et al.*—NRM 45184, 1, 53.5 mm SL. Central, arroyo Paray where crossing road Villeta-Villa Oliva. 14 Nov 1999. E. Åhlander *et al.*

Crenicichla "PARANÁ", Paraguay, río Paraná drainage, Alto Paraná: MHNG 2237.028. 5, 106.9–198.7 mm SL. Reserva Biológica de Itaipú (Tatí Yupí). 28 Jul 1984. C. Dlouhy.—MHNG 2474.096. 7, 84.0–132.9 mm SL. Río Itabó-guazú. 28 Jun 1989. C. Dlouhy.—MHNG 2474.097. 2, 65.3–127.0 mm SL. Reserva Biológica de Itaipú (inundated río Itabó-guazú). 28 Jun 1989. C. Dlouhy.—MHNG 2475.002. 2, 57.7–124.3 mm SL. Reserva Biológica de Itaipú (Tatí Yupí). 16 Jun 1989. C. Dlouhy.—MHNG 2475.013. 5, 110.2–133.6 mm SL. Río Limoy, Estancia Paloma. 13 Jun 1989. C. Dlouhy.—MHNG 2475.014. 3, 107.8–117.4 mm SL. Reserva Biológica de Itaipú (inundated río Itabó-guazú). 25 Jun 1989. C. Dlouhy.—MHNG 2475.017. 2, 71.9–72.7 mm SL. Reserva Biológica de Itaipú (inundated río Itabó-guazú). 22 May 1989. C. Dlouhy.—MHNG 2475.028. 1, 102.0 mm SL. Estancia Paloma. Jun–Jul 1989. C. Dlouhy.—MHNG 2475.029. 1, 71.3 mm SL. Arroyo León, tributary of río Limoy. 15 May 1989. C. Dlouhy.—MHNG 2475.036. 5, 103.2–141.1 mm SL. Lago Itaipú. May–Jun 1989. C. Dlouhy.—MHNG 2475.041. 1, 107.3 mm SL. Arroyo León, tributary of río Limoy. Jul 1989. C. Dlouhy.—MHNG 2475.041. 1, 107.3 mm SL. Arroyo León, tributary of río Limoy. Jul 1989. C. Dlouhy.—MHNG 2475.041. 1, 107.3 mm SL. Arroyo León, tributary of río Limoy. 15 May 1989. Lago Itaipú at Pyra-Pyta. 19 Feb 1983. C. Dlouhy.—MHNG 2730.055. 1, 157.5 mm SL. Lago Itaipú at Pyrapyta. 14 Jan 1983. C. Dlouhy.—MHNG 2730.065. 1, 157.6 mm SL. Río Paraná at Puerto Palma. 15 Aug 1980. C. Dlouhy.

Crenicichla sp. MHNG 2237.026, 1, 158.4 mm SL. Paraguay, Alto Paraná, río Monday, 30 km above the falls. 15 Mar 1984. C. Dlouhy.

Crenicichla sp. cf. *mandelburgeri*. NRM 46285. 6, 84.7–112.9 mm SL. Argentina, Misiones, arroyo Cuña Pirú. 24 Sep 1997. D. de Durana & H. Oñatibia.

Information on *C. hu* Piálek, Říčan, Casciotta & Almirón (2010), *C. tesay* Casciotta & Almirón (2008), *C. yaha* Casciotta, Almirón & Gómez (2006b), and *C. ypo* Casciotta, Almirón, Pialek, Gómez & Říčan (2010), was obtained from the respective descriptions only.

Crenicichla gillmorlisi, new species

Figs. 1–7, Tables 1–3

Holotype. MNHNP 126, adult female, 76.2 mm SL; Paraguay: Alto Paraná: río Acaray, dry arm below the reservoir. 15 May 1982. L. Naylor *et al*.

Paratypes. All from Paraguay, río Paraná drainage, río Acaray drainage.—Alto Paraná: MHNG 2237.036. 1, 105.8 mm SL. Lago Acaray. 3 May 1984. C. Dlouhy.—MHNG 2237.037. 1, 66.9 mm SL. Lago Acaray. 22 Jan 1983. C. Dlouhy.—MHNG 2237.066. 1, 110.7 mm SL. Lago Acaray. 25 Oct 1984. C. Dlouhy.— MHNG 2395.011. 6, 99.3–120.1 mm SL. Arroyo Yguazú at Juan E. O'Leary. 18 Oct 1987. C. Vaucher *et al.*— MHNG 2730.057. 2, 61.4–71.3 mm SL. Río Acaray, toll bridge. 12 Oct 1981. C. Dlouhy.—MHNG 2730.058. 1, 131.6 mm SL. Lago Acaray. 7 Sep 1982. C. Dlouhy.—MHNG 2730.059. 11, 40.6–94.8 mm SL. Río Acaray-cué below barrage. 15 May 1982. MHNG.—MHNG 2730.060. 1, ca 104 mm SL. Río Acaray below barrage. 9 Dec 1980. C. Dlouhy.—MHNG 2730.061. 1, 78.9 mm SL. Lago Acaray. Mar 1982. C. Dlouhy.—MHNG 2730.062. 2, 65.0–78.8 mm SL. Lago Acaray. 16 Oct 1982. C. Dlouhy.—MHNIB 0234, 2, 166-172 mm SL. Yguazú Reservoir at José D. Ocampos. 29 Feb 2012. O. Romero.—MNHNP 3686. 29, 25.2–82.6 mm SL. Same data as holotype.— NRM 42452. 1, 174.3 mm SL; NRM 42461, 2, 19.7–35.1 mm SL. Hernandarías, arroyo Paso Itá, Colonia Acaray, at balneario Paso Itá. 26 Feb 1998. S. O. Kullander & S. Rolón.—Caaguazú: NRM 41828, 1, 30.4 mm SL. Arroyo crossing at about 35 km on road Caaguazú–Yhú. 20 Mar 1998. E. Åhlander *et al.*

Diagnosis. Crenicichla gillmorlisi is recognized as distinct from all other species of Crenicichla by the colour pattern which develops as a row of paired vertical bars in young, and which are further fragmented into an adult colour pattern composed of small dark spots all over the sides. Distinguished from species of the C. lugubris and C. acutirostris groups, including C. vittata Heckel, by low number of E1 scales (42-57 vs. 80 or more); from species of the C. wallacii group by smooth vs. serrated supracleithrum; from species of the C. saxatilis group by absence vs. presence of a humeral blotch; from C. hemera Kullander and C. chicha Varella, Kullander & Lima (Varella et al. 2012) by infraorbitals 3 and 4 separate vs. co-ossified; from C. macrophthalma Heckel by fewer E1 scales (44-57 vs. 63–69), and cycloid vs. ctenoid cheek and predorsal scales; from the C. reticulata group, including C. semifasciata, by movable vs. rigidly implanted outer teeth, and nostril well separated from upper lip vs. close to upper lip (except in C. cyanonotus Cope in which nostril distinctly separated (Kullander 1986)); from the C. missioneira group by serrated vs. smooth preopercular margin. Similar in general aspect to other species of Crenicichla in the Paraguay and Paraná drainages and from the coast of Brazil, in particular to species with a juvenile or adult colour pattern composed of a row of narrow vertical bars along the middle of the side; among those, distinguished from Crenicichla "PARANÁ" in presence (vs. absence) of numerous small dark spots on sides, and less scales in E1 row (44-57 vs. 56-65); from C. jaguarensis Haseman, in the upper río Paraná, by presence of numerous narrow vertical bars in young specimens (vs. absence) and small spots present on sides in adults (vs. absence); from C. jupiaensis Britski & Luengo, in the upper and middle río Paraná, by lower jaw prognathous, vs. jaws isognathous, preopercular margin serrated vs. smooth, and by colour pattern, C. jupiaensis not developing a lateral band; from C. haroldoi Luengo, in the upper río Paraná, by preopercle serrated vs. commonly not serrated, and black dots marking lateral line scales absent vs. present; from C. mucuryna von Ihering, in the rio Mucuri, by low number of scales in E1 row (44-57 vs. 57-63) and serrated vs. smooth preopercular margin.



FIGURE 1. Crenicichla gillmorlisi, holotype, adult female, MNHNP 126, 76.2 mm SL. Río Acaray, dry arm below Lago Acaray.



FIGURE 2. *Crenicichla gillmorlisi*, paratypes. A. Juvenile, 30.4 mm SL, NRM 41828. B. Young, 41.6 mm SL, MNHNP 3686. C. Paratype, adult female, 73.9 mm SL, MNHNP 3686. D. adult female, 120.1 mm SL, MNHNG 2395.11. E. Adult male, 174.3 mm SL, NRM 42452.



FIGURE 3. *Crenicichla gillmorlisi.* Lower pharyngeal toothplate in occlusal, caudal, and lateral view. From MHNG 2730.058, 131.6 mm SL. Distance between tips of posterior processes 13.1 mm.

TABLE 1. Standard length (in millimeters) and proportional measurements in percents of standard length of *Crenicichla gillmorlisi*. SD, = standard deviation. Regression line parameters, a (intercept), b (slope), and r (Pearson's correlation coefficient) are calculated from measurements expressed in millimeters; shown when p<0.05. Holotype (HT) values given separately and also included in group values.

	HT	Ν	Min	Max	Mean	SD	a	b	r
Standard length (mm)	76.2	21	61.4	174.3	94.2	26.7			
Head length	29.3	21	28.3	33.2	30.5	1.4	2.390	0.278	0.990
Snout length	6.8	21	6.8	9.3	8.1	0.6	-1.688	0.100	0.988
Head depth	14.8	21	13.8	16.6	15.1	0.8	0.046	0.150	0.982
Body depth	22.1	21	19.8	25.0	22.0	1.2	-2.160	0.244	0.977
Orbital diameter	9.1	21	6.5	10.8	8.5	1.3	4.235	0.327	0.906
Interorbital width	5.1	21	4.7	7.9	5.6	0.8	-3.148	0.092	0.982
Pectoral-fin length	21.3	21	18.2	22.8	20.7	1.3	4.375	0.158	0.987
Upper jaw length	9.3	21	9.3	13.9	10.7	0.9	-3.337	0.144	0.977
Lower jaw length	13.9	21	12.7	16.2	14.4	0.8	-1.179	0.157	0.981
Caudal-peduncle depth	11.2	21	10.8	12.2	11.5	0.4	-0.937	0.125	0.995
Caudal-peduncle length	14.6	21	12.2	16.2	14.4	0.8	0.912	0.134	0.981
Last dorsal-fin spine length	13.5	20	10.9	14.0	12.7	0.9	2.215	0.102	0.977

TABLE 2. Frequency of scales in the E1 scale row in Crenicichla gillmorlisi, Crenicichla "PARANÁ" and C. mandelburgeri.

	Ν	42	44	45	46	47	48	49	50	51	52	53
Crenicichla "PARANÁ"	12											
Crenicichla gillmorlisi	22	1	1	4	4	3	2	5	2	4	1	2
Crenicichla mandelburgeri	33		1		2	4	3	1	8	4	3	3
TABLE 2. (Continued)	N	54	55	56	57	5	8	59	60	61	63	65
Crenicichla "PARANÁ"	12	51	55	1	1	2	0	1	2	2	2	1
Crenicichla gillmorlisi	22			-	1	-		-	_	_	_	-
Crenicichla mandelburgeri	33	1	2	1								

Distinguished from *C. tesay* (río Urugua-í, río Iguazú basin; Argentina and Brazil), *C. iguassuensis* Haseman (río Iguazú, Argentina and Brazil), *C. jurubi* Lucena & Kullander and *C. igara* Lucena & Kullander (upper río Uruguay in Brazil), which richly spotted, by narrow vertical bars or indistinct dark lateral band along the side vs. row of dark blotches along middle of side. Distinguished from *C. yaha* (río Urugua-í, río Iguazú) by lower jaw prognathous (vs. jaws isognathous), and colour pattern consisting of narrow vertical bars (young), or numerous dark spots on side, and variably expressed lateral band (vs. a row of large blotches close below upper lateral line); and from *C. hu* by light ground colour and narrow vertical bars (young), or numerous dark spots on side, and variably expressed lateral band (vs. dark grey or dark brown to black colour of body and fins, and 7–9 black irregular blotches on side).

Similar in spotted sides to coastal Brazilian species *C. lacustris* (Castelnau), *C. iguapina* Kullander & Lucena, *C. maculata* Kullander & Lucena, and *C. punctata* Hensel, differing in presence of vertical stripes in young specimens, and absence of blotches along the middle of the side vs. presence of a continuous dark lateral band or row of blotches and absence of narrow vertical stripes on the middle of the side at all sizes; distinguished from *C. lacustris*, and *C. iguapina* also by less scales in E1 row, 42–57 vs. 60–75.

Most similar to *C. mandelburgeri* in proportional measurements and meristics, but distinguished by the dissolution of vertical bars into small spots, absent in *C. mandelburgeri*.

Description. Largest male 174.3 mm SL, largest female 120.1 mm SL. Refer to Figures 1–3 for general aspect.

Head about as wide as deep. Caudal peduncle longer than deep. Snout moderately long, rounded from above, triangular in lateral view. Lower jaw slightly prognathous, its articulation below middle of orbit; ascending premaxillary processes reaching to 1/4 of orbit; maxilla reaching to or slightly beyond vertical from anterior margin of orbit. Lips thick and wide, lower lip folds separate anteriorly; folds of upper lip not continuous but cutting into a symphyseal wide thickening. Postlabial skin fold margin truncate. Orbit supralateral, not visible from below, chiefly in anterior half of head. Interorbital area flat, narrower than mouth. Nostril dorsolateral, closer to orbit than to margin of postlabial skin fold, with low tubular margin but no anterior marginal membranaceous skin flap. Preopercle with short, dense, regular serrations along vertical margin. Lateralis pores on head simple or with two small openings in small specimens, with multiple openings in larger specimens.

Flank scales ctenoid. All scales cycloid on head, on dorsum above anterior 1/3 of upper lateral line, along dorsal-fin base, on chest, and on belly below line from lower edge of pectoral-fin base to anal-fin origin. Predorsal scales small, embedded in skin, extending forward to transverse frontal lateralis canal. Prepelvic scales very small, deeply embedded in skin. Cheek naked anteroventrally; below eye about 8 scales, embedded in skin. Interopercle naked. Scales in E1 row 42–57 (Table 2). Transverse scale row counted from scale next to first anal-fin spine obliquely dorsad to dorsal-fin base with about 13–16 scales below and 5–6 scales above lateral line. Circumpeduncular scale rows 10–11 dorsally, 11–12 ventrally (23–25 including lateral lines).

Lateral-line scales 23/13(1), 24/10(1), 24/11(4), 24.12(7), 14/13(1), 25/10(1), 25/12(1), 25/13(1), 26/10(2), 26/12(1); 2 scales continuing lower line onto caudal fin; accessory lateral lines on caudal fin usually absent, occasionally one tubed accessory scale on caudal fin, between rays D3 and D4 or between rays V3 and V4, in one specimen three tubed scales between rays V3 and V4. Upper and lower lateral lines non-overlapping. Scales between upper lateral line and dorsal fin 10–12 anteriorly, $3\frac{1}{2}$ posteriorly; scale rows between lateral lines 3. Anterior upper lateral-line scales not much larger than adjacent scales, remaining lateral-line scales nearly same size as adjacent scales; two scales impinging on each scale of anterior part, one on each scale of posterior part of upper lateral line; $1-\frac{1}{2}$ scales impinging on each scale of lower lateral line. Dorsal, anal, pectoral and pelvic fins without scales. Caudal-fin squamation extending to about $\frac{1}{3-\frac{1}{2}}$ of fin, posterior margin of scaled area straight vertical.

First dorsal-fin spine about 1/4–1/3 length of last; spines subequal in length from 6th–9th. Soft part of dorsal fin with rounded or subacuminate tip, reaching to base of caudal fin or slightly beyond. Dorsal-fin rays XIX.12 (1), XX.12 (1), XXI.11 (4), XXI.12 (20), XXII.11 (8), XXII.12 (2). Soft anal fin with rounded tip, reaching to or slightly beyond base of caudal fin. Anal-fin rays III.7 (6), III.8 (21), III.9 (1). Caudal fin rounded. Pectoral fin rounded, 6th or 7th ray longest, reaching about halfway to spinous anal fin. Pectoral-fin rays 15 (1), 16 (18), 17 (2). Pelvic fin inserted well posteriorly to vertical from pectoral axilla, with subacuminate tip, second ray longest, reaching about halfway to soft anal fin.

All teeth pointed, recurved, teeth in outer row movable but not depressible, teeth in inner rows depressible. Outer row teeth slightly larger than inner teeth. Outer row of teeth in upper jaw extending for nearly the length of the alveolar ramus of the premaxilla. Upper jaw with 3–4 inner rows anteriorly, one inner row continued almost as long as outer row. Outer row of teeth in lower jaw extending along 3/4 of length of jaw. Lower jaw with 2–3, occasionally 4 inner rows anteriorly, one inner row continued posteriorly for half the length of the outer row.

Gill rakers externally on first gill arch 1 (1), 2 (19), 3 (2) epibranchial, 1 in angle, 5 (1), 8 (17), 9 (4) ceratobranchial. Gill rakers on lower pharyngeal tooth-plate 8 (2), 9 (4), 10 (4), 11 (6), 13 (3). Microbranchiospines present externally on 2^{nd} to 4th arches.

Lower pharyngeal tooth-plate (Fig. 3) dissected from a 131.6 mm specimen (MHNG 2730.058), relatively compressed dorsoventrally, with moderately long posterior and anterior processes; tooth-plate length 84% of width; dentigerous area length 70% of width; 22 teeth in posterior row, 7–8 teeth in median row. All teeth compressed, except posteromedian, which almost circular in cross section. Anterior teeth slender, erect or slightly inclined, with recurved tip, shape changing gradually in symphysian rows, posterior teeth more stout and with posterior straight cusp. Teeth along margin much shorter than median teeth, bevelled; teeth along posterior margin of bone with antrorse posterior cusp and slightly cuspidate anterior bulge.

Vertebral counts 16-17+18-20=35-37 (Table 3).

Coloration in preservative. Smallest specimen, 25.2 mm SL (MNHNP 3686), pale yellowish with five brown vertical bars extending from dorsal midline across side, and dull blotch on side of caudal peduncle; anteriormost bar narrow, entire; posterior bars broad, each split below upper lateral line by narrow light vertical stripe. Caudal ocellus present as small black spot surrounded by hyaline ring. Slightly larger juveniles (NRM 41828, 42461; Fig.

2A) whitish with brown stripe from lower jaw to orbit. Postorbital brown stripe from orbit horizontal to tip of opercle. Brown band paralleling postorbital stripe slightly dorsal to it. Two contiguous dark stripes on each side of midline of top of head. Brown band along middle of side, enforced at intervals by double vertical bars extending down from dorsal-fin base. Indistinct narrow dark band along abdominal side. Brown blotch at base of caudal fin, in 30.4 mm specimen followed by chevron shaped black mark and short brownish stripe along middle rays, in 35.1 mm specimen by small black spot surrounded by hyaline ring and narrow vertical stripes, representing incipient ocellated blotch. Suborbital stripe absent in juveniles.

Abdominal	16		17			18		Ν
Caudal	19	20	18	19	20	18	19	
Crenicichla "PARANÁ"	1	1		4	2		5	13
Crenicichla gillmorlisi	3	2	4	6	3			18
Crenicichla mandelburgeri	5			10	2	1		18

TABLE 3. Frequency of vertebral counts in Crenicichla gillmorlisi, Crenicichla "PARANÁ" and C. mandelburgeri.

Young specimens from about 40 mm SL (Fig. 2B) with short or incipient suborbital marking. Lateral band absent, replaced by series of about 8–9 pairs of brown vertical bars. Ocellated, elongate blotch at caudal-fin base.

Adults (Fig. 1, 2C–E), about 60 mm SL and larger, with off-white, pale grey, or light brownish ground colour. Dorsum not noticeably darker than sides. Chest whitish, abdomen, body close to anal-fin base, and ventral margin of caudal peduncle off-white to faint yellowish. Dorsal part of head, snout and lips greyish, nape slightly lighter, brownish with darker brown blotch on each side anterior to extrascapulars. Sides of head, below eye pale brownish, lighter ventrally. Postorbital dark brown stripe from orbit to opercular tip. Suborbital stripe present, narrow, always strongly contrasted, solid or composed of small spots, extending obliquely from lower margin of orbit to or almost to inner margin of lower limb of exposed preopercle. More or less distinct greyish or brownish preorbital stripe from orbit to upper lip. On each side, vertical bars in young and juveniles transformed into 3–5, usually four short segments, in the largest specimen about nine irregular horizontal rows of small spots. Along dorsum may be present five indistinct dark vertical blotches, first below origin of dorsal fin, last below soft dorsal fin. Lateral markings usually expressed as short horizontally extended blotches; in three specimens 110.7–174.3 (MHNG 2730.058, 2237.066, NRM 42452) relatively smaller and rounded (Fig. 2E). Indistinct lateral band can be traced along middle of side in most specimens, but best expressed in MHNG 2395.11 (Fig. 4D). Dorsal fin semihyaline; spinous portion with faint or distinct small dark spots arranged in two well defined rows; soft portion with 2-4 rows of small spots. Anal fin semihyaline to pale greyish with up to six rows of small dark spots on soft portion. Caudal fin brownish basally, semihyaline posterior to scaly portion, with 4–7 rows of small dark spots across fin and posterior margin greyish. Small round black blotch at base of caudal fin, immediately dorsal to lateral line scales, surrounded by yellowish ring. Caudal-fin blotch indistinct and not ocellated in largest specimen (Fig. 2E). Pelvic fin whitish.

Only one specimen, 120.1 mm SL (Fig. 2D) showing colour pattern characteristic of breeding female *Crenicichla*. Spots in fins absent or indistinct. A large indistinct brown, elongate blotch distally on dorsal fin between spines 14 and 17. In this specimen, spots apparently absent from sides, and middle of side with series of short vertical bars. Scales with highlighted pale bases and brownish margin. Black caudal-fin blotch not ocellated.

Live coloration. A freshly collected adult, probably male specimen (Fig. 4) shows colour pattern similar to preserved specimens, differing chiefly in olivaceous sheen on sides.

Comparative morphometrics. Bi-plots and PCA did not show any diagnostic differences between samples of *C. gillmorlisi, C. mandelburgeri*, and *Crenicichla* "PARANÁ". *Crenicichla gillmorlisi*, however, has slightly wider interorbital space, especially in larger specimens, yielding a slope significantly different from that of *Crenicichla* "PARANÁ" and *C. mandelburgeri*, as showing clearly in comparison with head length (Fig. 5). Proportionally, there is considerable overlap, with 15.3–22.7 % of head length (N= 12 mean 18.1, standard deviation 2.0) in *C*. "PARANÁ", 15.1–26.0 % of head length (N= 21, mean 18.5, standard deviation 3.3) in *C. gillmorlisi*, and 13.5–19.3 % of head length (N= 28, mean 16.1, standard deviation 1.5) in *C. mandelburgeri*. Proportional measurements for *C. mandelburgeri* were reported by Kullander (2009), and are given here (Table 4) for Paraguayan *Crenicichla* "PARANÁ".

No significant differences were found in meristic data between *C. gillmorlisi* and *C. mandelburgeri*. *Crenicichla* "PARANÁ", however, tends to higher scale and abdominal vertebral counts (Tables 2–3) than both *C. gillmorlisi* and *C. mandelburgeri*.



FIGURE 4. *Crenicichla gillmorlisi*. Adult, probable male, 137.0 mm SL. MHNIB 0234. Yguazú Reservoir at José D. Ocampos. Freshly collected 28–29 Feb 2012. Photo by Walter A. Gill Morlis A.

TABLE 4. Standard length (in millimeters) and proportional measurements in percents of standard length of *Crenicichla* "PARANÁ". SD= standard deviation. Regression line parameters, a (intercept), b (slope), and r (Pearson's correlation coefficient) are calculated from measurements expressed in millimeters; shown when p<0.05.

	N	Min	Max	Mean	SD	a	b	r
Standard length (mm)	12	71.9	198.7	128.6	30.0			
Head length	12	28.7	32.8	30.4	1.1	-0.854	0.311	0.987
Snout length	12	8.3	11.3	9.5	0.9	-3.694	0.125	0.975
Head depth	12	13.1	17.5	14.5	1.2	-2.128	0.163	0.950
Body depth	12	19.1	24.0	21.1	1.4	-1.117	0.220	0.961
Orbital diameter	12	5.8	9.0	7.2	0.8	3.591	0.042	0.930
Interorbital width	12	4.7	6.9	5.5	0.6	-3.305	0.082	0.977
Pectoral-fin length	12	17.0	20.3	18.8	1.0	0.523	0.182	0.978
Upper jaw length	12	10.2	13.9	11.7	1.2	-5.826	0.165	0.980
Lower jaw length	12	14.4	17.6	15.9	0.9	-3.042	0.184	0.982
Caudal-peduncle depth	12	10.0	12.0	10.7	0.6	-1.812	0.121	0.981
Caudal-peduncle length	12	12.9	14.7	13.9	0.6	1.932	0.124	0.980
Last dorsal-fin spine length	11	10.5	13.5	11.6	0.8	3.429	0.088	0.983

Geographical distribution and habitats. All localities of *C. gillmorlisi* are located in the río Acaray drainage in Paraguay (Fig. 6). The Acaray has two major branches, and the right branch is known as río or arroyo Yguazú. Habitat information is available only for the NRM samples obtained during high water levels. At Paso Itá near Hernandarías (Fig. 7) one adult and two young *C. gillmorlisi* were captured in a small stream with brownish very turbid water, with moderate current, about 4 m wide and 1–1.5 m deep. The landscape was open agriculture, with mainly grass vegetation. The bottom substrate consisted of rocks and stones. Fishing was made by seining along about 100 m of stream to 80 cm depth. Fishes were found only along overhanging banks. The most common associated species were *Gymnogeophagus setequedas* Reis, Malabarba & Pavanelli (Cichlidae) and *Bryconamericus stramineus* Eigenmann (Characidae). Other species were identified as *Astyanax* sp. (Characidae), *Hypostomus dlouhyi* Weber, *Hypoptopoma* sp. (Loricariidae), *Hoplias* sp. (Erythrinidae), *Leporinus lacustris* Amaral Campos (Anostomidae), *Steindachnerina brevipinnis* (Eigenmann & Eigenmann) (Curimatidae), *Eigenmannia virescens* (Valenciennes) (Sternopygidae), *Crenicichla lepidota* (Cichlidae), and *Pyrrhulina australis* Eigenmann & Kennedy (Lebiasinidae).

At Yhú a juvenile was collected in a small stream, more than 1.5 m deep with running, dark and turbid water,

in open landscape with low trees and grass. Fishing was done with hand nets and seine in vegetation and on a small beach. The bottom consisted of sand. The most common associated species were *Characidium* sp. (Crenuchidae) and *Bryconamericus stramineus* (Characidae). Other species were identified as *Astyanax* sp., *Cheirodon* sp., *Hemigrammus* sp., *Mimagoniates microlepis* (Steindachner) (Characidae), *Corydoras diphyes* Axenrot & Kullander (Callichthyidae), *Bunocephalus* sp. (Aspredinidae), *Gymnogeophagus setequedas* (Cichlidae), *Hypoptopoma* sp., (Loricariidae), and *Phallotorynus victoriae* Oliveros (Poeciliidae).

Crenicichla lepidota was also collected together with MHNG 2237.66 (lago Acaray) and MHNG 2395.11 (Juan E. O'Leary).

Etymology. This species is named for ichthyologist Walter A. Gill Morlis A., fisheries officer of the Itaipú Binacional, Ciudad del Este, Paraguay, who contributed considerably to the PROVEPA surveys of fishes in tributaries of the Paraná River, and in special recognition of his strong long term engagement in the inventory of the fishes of the río Paraná.



FIGURE 5. Biplot of interorbital width against head length in *Crenicichla gillmorlisi* ($r^2=0.957$), *C.* "PARANÁ" ($r^2=0.944$), and *C. mandelburgeri* ($r^2=0.897$). The slope of *C. gillmorlisi* is significantly different from those of *C. mandelburgeri* (p=0.001), and *C.* "PARANÁ" (p=0.033).

Discussion

The large specimen NRM 42452, 174.3 mm SL (Fig. 2E) has more E1 scales (57) than the other specimens (42–53) of *C. gillmorlisi*, overlapping with the lower extreme of *C.* "PARANÁ" (Table 2: 56–65). The two juveniles 19.7 and 35.1 mm SL from the same locality have about 46 and 48 E1 scales, respectively, which is within the range of

other *C. gillmorlisi*. Also, the colour pattern with small spots agrees with *C. gillmorlisi* rather than with *C.* "PARANÁ", which never shows small spots on the side. We consequently refer the specimen to *C. gillmorlisi*.

The río Acaray has two barrages along its course. The Acaray hydroelectric power plant is located close to the mouth of the río Acaray into the río Paraná, and is in operation since 1968. Some distance upstream the flow of the river is regulated by the Yguazú reservoir, completed in 1977. Upstream movements of fishes from the Paraná are thus probably limited, whereas downstream leakage may be expected to occur. It is thus not unexpected to find *C. gillmorlisi* both upstream and downstream the Acaray hydroelectric power plant, as there is quite some stretch of river between the barrage and the mouth. The Acaray empties into the Paraná some distance downstream of the Itaipú reservoir, which was closed in 1982. Whereas *Crenicichla* "PARANÁ" is common in the Itaipú reservoir, from Guairá downstream to the Itaipú dam, *C. gillmorlisi* has only been recorded from the Acaray drainage.

Tributaries to the río Paraná upstream from the Entre Ríos wetlands in Argentina have yielded several fish species each known only from one or a few of them. Several potentially endemic cichlid species of the genera Crenicichla and Australoheros Říčan & Kullander have been described recently from the Iguazú and Urugua-í drainages in Argentina (Casciotta et al. 1995, 2000, 2006a, b, 2010; Pialek et al. 2010) and from tributaries in Paraguay (Říčan & Kullander 2008; Kullander 2009), in addition to the previously described C. iguassuensis from the rio Iguaçu in Brazil. Gymnogeophagus setequedas was based on specimens from the Acaray and Monday drainages, but also reported from tributaries upstream of the Itaipú barrage to the río Carapá (Reis et al. 1992). The type locality of G setequedas is the same as the locality of the paratypes of C. gillmorlisi MHNG 2395.011. Cichlasoma pusillum Kullander (1983) was described from the lower Itaipú reservoir (type locality, Puerto Palmas), río Acaray and nearby río Uruguay. The latter are re-identifed as C. dimerus (Kullander, unpublished). Recently collected material is available from the Yguazú reservoir and the río Monday (NRM 42271, 42333, 45255). Australoheros guarani Říčan & Kullander (2008) is based on specimens from the upper río Monday and río Tembey. Although there is a strong tendency for species in Paraná tributaries to be restricted to one or a few rivers above the falls or rapids in the lower course, collections in Paraguayan tributaries of the Paraná are still relatively few. It seems possible that C. gillmorlisi may also occur in the río Monday, or even other nearby rivers. At present only one specimen of Crenicichla other than C. lepidota is recorded from the Monday, viz. MHNG 2237.026, approximately 158 mm SL, a very large probable female, curved, with open mouth and somewhat faded colours. It shows a faint lateral band with traces of narrow vertical stripes, and small spots typical of C. gillmorlisi are absent on the body. It tentatively represents C. mandelburgeri.

Bi-plots and Principal Component Analysis of measurement data of C. gillmorlisi, C. mandelburgeri, and Crenicichla "PARANÁ" did not show any diagnostic differences between species samples, and relatively minor intraspecific variation. Larger specimens of C. gillmorlisi may have somewhat wider interorbital space than Crenicichla "PARANÁ" and C. mandelburgeri (Fig. 5). Interorbital width in Crenicichla may reflect age and growth pattern. Lucena & Kullander (1992) speculated that a relatively wide interorbital may reflect positive size allometry in adult specimens with reduced length growth, and a narrow interorbital would be correlated with active growth and thus an indicator of small length or paedomorphy. The size range of the type series of C. gillmorlisi, with the largest specimen 174.3 mm SL, exceeds that of C. mandelburgeri, of which the largest specimen was 114.6 mm SL. Crenicichla "PARANÁ" is apparently a larger species than C. mandelburgeri and C. gillmorlisi, with specimens up to about 200 mm SL, and thus expected to be in active length growth phase at sizes of adult C. mandelburgeri. The difference in length distribution may reflect a collecting bias, because more specimens, from more localities, are available of C. gillmorlisi. Most C. mandelburgeri were apparently taken by active fishing in running water, probably resulting in a bias toward smaller specimens. Most C. "PARANÁ" were taken by gill nets in lake conditions, and that may have favoured large specimens. Many specimens of C. gillmorlisi show signs of gillnetting and several samples were definitely taken with active methods (seine, rotenone), perhaps explaining the wide length distribution. Crenicichla gillmorlisi does not differ in meristic data from C. mandelburgeri. Crenicichla "PARANÁ", however, has more scales in the E1 row, and usually one more abdominal vertebra than C. gillmorlisi and C. mandelburgeri.

Consequently, based on available data, *C. gillmorlisi* can be diagnosed from *C. mandelburgeri* only by the colour pattern of young and adults, as *C. mandelburgeri* is not known to develop any spots or blotches, but instead presents a distinct lateral band. Juveniles of *C. gillmorlisi* at the size of Fig. 2A strongly resemble juvenile *Crenicichla* from within the range of *C. mandelburgeri*, and larger ontogenetic series are needed of both species to investigate diagnostic characters in juveniles. Consequently, juveniles of *C. mandelburgeri* and *C. gillmorlisi* are

here recognized as such only by co-occurrence with adults. This, incidentally, implies a reservation the identity of the juveniles of *C. mandelburgeri* from the río Pirayuy reported by Kullander (2009) as no adult *C. mandelburgeri* are known from that locality. Actually, for most or all species of *Crenicichla* species diagnostic characters are known only from adults or subadults, and not from early ontogenetic stages.

Short doubled vertical bars along the middle of the side, as seen in young *C. gillmorlisi* occur also in young *C. mandelburgeri*, (Kullander 2009: figs. 2–3) and young and adult *Crenicichla* "PARANÁ" (Kullander 1981: fig. 6), but occurs also in adult *C. haroldoi* and *C. jupiaensis* in the upper rio Paraná in Brazil. Outside the Paraná basin, a similar pattern occurs in adult *C. mucuryna* from the coastal rio Mucuri in Brazil (Kullander & Lucena, 2006: fig. 1). None of these species is known to develop a colour pattern with spots similar to that of *C. gillmorlisi*. However, the similarity in colour between young *C. gillmorlisi* and adult *C. mucuryna* is striking. *Crenicichla mucuryna* is restricted to one short coastal drainage in Minas Gerais, east of the upper Paraná and São Francisco rivers. In a revision of coastal Brazilian *Crenicichla* Kullander & Lucena (2006) redescribed the species and considered it unrelated to the other coastal species, and more similar to species in the Paraná drainage. This similarity is primarily expressed in the colour pattern, and a relationship analysis is outstanding.



FIGURE 6. Map of eastern Paraguay showing geographical distribution of *Crenicichla gillmorlisi*, based on collecting localities, all in the río Acaray drainage in Paraguay.



FIGURE 7. Habitat of Crenicichla gillmorlisi at Paso Itá, Hernandarías, Paraguay.

Several species of the coastal *C. lacustris* species group, revised by Kullander & Lucena (2006), however, particularly *C. lacustris*, *C. iguapina*, and *C. punctata*, are extensively spotted on the sides and fins, and in *C. punctata* and *C. lacustris* also on the head. Those species, however, do not present a pattern of narrow vertical bars as in *C. gillmorlisi*. Species from the left bank of the Paraná, *C. iguassuensis* Haseman, from the río Iguazú, and *C. tesay* Casciotta & Almirón (2008), from the Urugua-í and Iguaçu rivers, and *C. jurubi* and *C. igara* in the upper Uruguay drainage (Lucena & Kullander 1992) are also marked by small dark spots, but these species have in common a pattern of large blotches immediately below the level of the lateral line shared uniquely with other species from the Urugua-í and Iguazú (*C. yaha*), and Piray-miní (*C. hu*), and seem to be part of a different evolutionary lineage.

Double vertical bars or blotches are also present in young *C. semifasciata* and similar species in the *C. reticulata* species group in the Amazon, Orinoco and Essequibo drainages. *Crenicichla semifasciata* differs considerably in body shape and dentition from other *Crenicichla* in the Paraguay-Paraná, Uruguay, and coastal Uruguayan and Brazilian drainages. The body is more stout, the head conspicuously wide, and the snout short and broad. The teeth are relatively well spaced with an outer row of rigidly implanted large canines, and only 1–3 inner sparse rows, of smaller, also non-depressible teeth. *Crenicichla semifasciata* was previously in the genus *Batrachops* Heckel together with northern South American species with similar shape, colour pattern, and dentition. Because many species of *Crenicichla*, including the *C. wallacii, C. lugubris, C. acutirostris, C. saxatilis* species groups are characterized by a horizontal stripe and absence of vertical bars, double vertical bars may be a relationship indicator, but reflects also the usual colour pattern in South American cichlids, which is barred rather than striped.

Although the spots on body and fins provide an easy field identification of *C. gillmorlisi*, it seems, based on a single specimen (Fig. 2D), that breeding females may have a more uniform colour, with spots obsolete or absent. Such sexual dimorphism is shared with other *Crenicichla*. Breeding females may therefore be difficult to separate from females of *C. mandelburgeri* and *Crenicichla* "PARANÁ", or even other species of *Crenicichla*. A conspicuous ocellated blotch in the dorsal fin is a marking characteristic of adult female *Crenicichla*, although it is not known if this mark may vary with reproductive status. In the present material, only one of the specimens (Fig. 2D), also the only specimen consequently identified potentially as a breeding female, presents a blotch in the dorsal fin and only indistinctly.

Pending a phylogenetic analysis of southern South American *Crenicichla*, the best relationship hypothesis for *C. gillmorlisi* may be that it is most closely related to *C. mandelburgeri*, from which it apparently differs only in colour pattern, and part of a assemblage also including *C. jupiaensis*, *C. haroldoi*, and *C. "PARANÁ"*. The upper Paraná species *C. jaguarensis* has narrow vertical bars crossing a distinct lateral band, but they are apparently simple, not doubled as in *C. gillmorlisi*.

Crenicichla gillmorlisi and *C*. "PARANA" were not included in the molecular analysis of middle Paraná *Crenicichla* by Piálek *et al.* (2012) judging from their localities, which do not include the río Acaray or the Itaipú reservoir. The species that they call *C*. '*Parana*', from near the Yacyretá reservoir, is independently labelled with the same code name.

Piálek *et al.* (2012) report two clades which they identify as *C. mandelburgeri* and *C.* aff. *mandelburgeri*, both sampled from approximately opposite tributaries on both sides of the Paraná in Paraguay and Argentina, *C.* aff *mandelburgeri* from slightly more downstream the Paraná, but both present in the arroyo Tabay. Kullander (2009) noticed differences between samples of adults from the Poromoco and Tembey rivers, but was unable to find diagnostic morphometric, meristic, and chromatic characters; nonetheless species distinctness may be indicated in the molecular phylogeny of Piálek *et al.* (2012). The paratypes of *C. mandelburgeri* from the río Pirayuy are juveniles and of limited use for screening diagnostic characters, but conforming in available characters with Tembey and Poromoco samples. Pialék *et al.* identify a sample from the río Pirayuy as *C. aff. mandelburgeri*. They identify two samples from the río Tembey (type locality drainage) as *C. mandelburgeri*. From their discussion about the status of *C. niederleinii* (our *C. "PARANÁ"*, from the Itaipú reservoir), it is obvious that Pialék *et al.* (2012) have misidentified their *C. aff. mandelburgeri* (from the río Cuñapirú in Argentina to Yacyretá tributaries) as being the same species, probably a consequence of not having specimens of *C. "PARANÁ"*. We examined specimens from the río Cuñapirú (NRM 46285), the mouth of which is opposite that of the río Pirapó in Paraguay. They are similar to the type series of *C. mandelburgeri* in counts, measurements and colour pattern.

With C. gillmorlisi, seven species of Crenicichla have been recognised in Paraguay. At least two species have

not been formally described, one of them *Crenicichla* "PARANÁ". *Crenicichla mandelburgeri* sensu Kullander (2009) may be a composite as suggested by DNA data (Pialék *et al.* 2012) and more extensive sampling may be more informative about species boundaries. *Crenicichla jupiaensis* was reported by Casciotta *et al.* (2007) from Yahapé on the Argentinian side of the Paraná downstream of the Yacyretá reservoir, and may consequently also be found in Paraguayan waters. This species is otherwise known only from the Paraná basin upstream from the former Guairá falls. It is also noteworthy that several tributaries of the Paraná in Paraguay have not been extensively sampled, and additional species may be present.

Acknowledgements

NRM specimens were collected during surveys conducted by NRM and MNHNP under the Proyecto Vertebrados del Paraguay (PROVEPA), financed by the Swedish International Development Agency 1992–1999. Darío Mandelburger, Mirtha Medina R., Selvando Rolón (MNHNP), Walter A. Gill Morlis A. (Itaipú Binacional, Ciudad del Este), and Erik Åhlander (NRM) participated in field activities. Volker Mahnert and Sonia Fisch-Müller (MHNG) made available MHNG collections. Walter Gill Morlis kindly made available information and images of freshly collected specimens of *C. gillmorlisi*. Henrique R. Varella made numerous constructive comments on the manuscript. Frederick Bauer (MNHNP) assisted with MNHNP catalog numbers. CAS holds a position as fellow researcher of the CNPq, Brazil.

Literature cited

- Casciotta, J., Almirón, A., Bechara, J., Ruiz Diaz, F., Sanchez, S. & González, A. (2007) First record of *Crenicichla jupiaensis* Britski & Luengo, 1968 (Perciformes: Cichlidae) in freshwaters of Argentina. *Ichthyological Contributions of Peces Criollos*, 4, 1–4.
- Casciotta, J.R., Almirón, A.E. & Gómez, S.E. (2006a) A new species of *Australoheros* (Teleostei: Perciformes: Cichlidae) from the río Iguazú basin, Argentina. *Zoologische Abhandlungen*, 55, 77–83.
- Casciotta, J.R., Almirón, A.E. & Gómez, S.E. (2006b) *Crenicichla yaha* sp. n. (Perciformes: Labroidei: Cichlidae), a new species from the río Iguazú and arroyo Urugua-í basins, northeastern Argentina. *Zoologische Abhandlungen*, 56, 107–112.
- Casciotta, J.R., Gómez, S.E. & Toresani, N.I. (1995) 'Cichlasoma' tembe, a new cichlid species from the río Paraná basin, Argentina (Osteichthyes, Labroidei). Ichthyological Exploration of Freshwaters, 6, 193–200.
- Casciotta, J.R., Gómez, S.E. & Toresanni, N.I. (2000) *Gymnogeophagus che*, una nueva especie de la familia Cichlidae de la cuenca del río Paraná (Perciformes, Labroidei). *Revista de Museo Argentino de Ciencias Naturales, nueva série*, 2, 53–59.
- Casciotta, J.R., Almirón, A.E., Piálek, L., Gómez, S.E. & Říčan, O. (2010) Crenicichla ypo (Teleostei: Cichlidae), a new species from the middle Paraná basin in Misiones, Argentina. Neotropical Ichthyology, 8, 643–648. http://dx.doi.org/10.1590/S1679-62252010000300009
- Falster, D.S., Warton, D.I. & Wright, I.J. (2006) SMATR: Standardised major axis tests and routines, ver. 2.0. Available from http://www.bio.mq.edu.au/ecology/SMATR/ (accessed 27 March 2013)
- Kullander, S.O. (1981) Cichlid fishes from the La Plata basin. Part I. Collections from Paraguay in the Muséum d'Histoire naturelle de Genève. *Revue suisse de Zoologie*, 88, 675–692.
- Kullander, S.O. (1982) Cichlid fishes from the La Plata basin. Part III. The *Crenicichla lepidota* species group. *Revue suisse de Zoologie*, 89, 627–661.
- Kullander, S.O. (1983) A revision of the South American cichlid genus Cichlasoma (Teleostei: Cichlidae). Swedish Museum of Natural History, Stockholm, 296 pp.
- Kullander, S.O. (1986) *Cichlid fishes of the Amazon River drainage of Peru*. Swedish Museum of Natural History, Stockholm, 431 pp.
- Kullander, S.O. (2003) Family Cichlidae (Cichlids). *In*: Reis, R.E., Kullander, S.O. & Ferraris Jr., C.J. (Eds.), *Check list of the freshwater fishes of South and Central America*. Edipucrs, Porto Alegre, pp. 605–654.
- Kullander, S.O. (2009) *Crenicichla mandelburgeri*, a new species of cichlid fish (Teleostei: Cichlidae) from the Paraná river drainage in Paraguay. *Zootaxa*, 2006, 41–50.
- Kullander, S.O. & Lucena, C.A.S. (2006) A review of the species of *Crenicichla* (Teleostei: Cichlidae) from the Atlantic coastal rivers of southeastern Brazil from Bahia to Rio Grande do Sul States, with descriptions of three new species. *Neotropical Ichthyology*, 4, 127–146.

http://dx.doi.org/10.1590/S1679-62252006000200001

Kullander, S.O., Norén, M., Friðriksson, B. & Lucena, C.A.S. (2010) Phylogenetic relationships of species of *Crenicichla* (Teleostei: Cichlidae) from southern South America based on the mitochondrial cytochrome *b* gene. *Journal of Zoological*

Systematics and Evolutionary Research, 48, 248–258.

- Lucena, C.A.S. (2007) Two new species of the genus *Crenicichla* Heckel, 1840 from the upper rio Uruguay drainage (Perciformes: Cichlidae). *Neotropical Ichthyology*, 5, 449–456. http://dx.doi.org/10.1590/S1679-62252007000400004
- Lucena, C.A.S. & Kullander, S.O. (1992) The *Crenicichla* species of the Uruguai River drainage in Brazil. *Ichthyological Exploration of Freshwaters*, 3, 97–160.
- Piálek, L., Říčan, O., Casciotta, J. & Almirón, A. (2010) *Crenicichla hu*, a new species of cichlid fish (Teleostei: Cichlidae) from the Paraná basin in Misiones, Argentina. *Zootaxa*, 2537, 33–46.
- Piálek, L., Říčan, O., Casciotta, J., Almirón, A. & Zrzavý, J. (2012) Multilocus phylogeny of *Crenicichla* (Teleostei: Cichlidae), with biogeography of the *C. lacustris* group: Species flocks as a model for sympatric speciation in rivers. *Molecular Phylogenetics and Evolution*, 62, 46–61. http://dx.doi.org/10.1016/j.ympev.2011.09.006

Reis, R.E., Malabarba, L.R. & Pavanelli, C.S. (1992) *Gymnogeophagus setequedas*, a new cichlid species (Teleostei: Labroidei) from middle rio Paraná system, Brazil and Paraguay. *Ichthyological Exploration of Freshwaters*, 3, 365–272.

- Říčan, O. & Kullander, S.O. (2008) The Australoheros (Teleostei: Cichlidae) species of the Uruguay and Paraná River drainages. Zootaxa, 1724, 1–51.
- Varella, H.R., Kullander, S.O. & Lima, F.C.T. (2012) Crenicichla chicha, a new species of pike cichlid (Teleostei: Cichlidae) from the rio Papagaio, upper rio Tapajós basin, Mato Grosso, Brazil. Neotropical Ichthyology, 10, 233–244. http://dx.doi.org/10.1590/S1679-62252012000200002