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DESCRIPTION OF TWO NEW SPECIES OF *Crenicichla* (TELEOSTEI: CICHLIDAE) FROM THE LOWER IGUAZÚ RIVER WITH A TAXONOMIC REAPPRAISAL OF *C. iguassuensis*, *C. tesay* AND *C. yaha*

Descripción de dos nuevas especies de Crenicichla *(Teleostei: Cichlidae) del bajo río Iguazú con la revisión taxonómica de* C. iguassuensis, C. tesay *y* C. yaha

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Resumen. Cinco especies de *Crenicichla* se conocen en la actualidad del río Iguazú inferior. Cuatro de ellas son endémicas (miembros del complejo de especies *C. mandelburgeri* del grupo *C. lacustris*) y viven en simpatría; la quinta especie (*C. lepidota*) pertenece al grupo de especies de la cuenca Amazonas/Orinoco (*C. saxatilis*) y está lejanamente relacionada a las restantes especies. Las cuatro especies simpátricas, difieren sustancialmente en la morfología de la cabeza/dientes y la utilización relativa de los nichos ecológicos. Además representan todos los ecomorfos conocidos dentro de *Crenicichla*. Dos de ellas son aquí descriptas como nuevas especies, *C. tapii* sp. n. gregaria, de boca pequeña, recolectora entre la vegetación y *C. tuca* sp. n. de boca grande y labios gruesos, exploradora/excavadora de cavidades. La especie piscívora de boca grande *C. iguassuensis* representa la forma ancestral del género. La cuarta especie es la recolectora de moluscos de boca pequeña *C. tesay* con una mandíbula faríngea inferior robusta con dientes molariformes. Poblaciones referidas en estudios anteriores a *C. yaha* son reclasificadas como *C. tesay*. *Crenicichla yaha* es una especie endémica de la vecina cuenca del arroyo Urugua-í, conocida solo por nueve especímenes colectados en 1989 (antes que la represa fuera construída en este arroyo). El estatus taxonómico de las poblaciones referidas aquí a *C. iguassuensis* es tentativo porque éstas forman un clado separado en el análisis de ADN mitocondrial, revelando escasas diferencias morfológicas, una amplia separación en su distribución respecto de la localidad tipo y presencia de formas similares aun no descriptas en el área intermedia.

Palabras clave. Áreas de endemismo, diversificación morfológica, cuenca del Río de La Plata, Paraná, grupo de especies

Abstract. Five species of *Crenicichla* have been recorded so far from the lower Iguazú River. Four of them are endemic (members of the *C. mandelburgeri* species complex from the *C. lacustris* group) and living in sympatry; the fifth species (*C. lepidota*) belongs to an Amazon/Orinoco-centered species group (C. *saxatilis*) and is only distantly related to the remaining species. The four sympatric species differ substantially in their head/teeth morphology and related utilization of the ecological niches, and represent all known ecomorphs within *Crenicichla.* Two of them, a gregarious small-mouthed picker/grazer *C. tapii* sp. n. and a large-mouthed thick-lipped cavity explorer/excavator *C. tuca* sp. n. are described here as new species. The piscivorous large-mouthed species *C. iguassuensis* represents the ancestral form of the genus. The fourth species is the small-mouthed picker/molluscivore *C. tesay* with a robust lower pharyngeal jaw with molariform teeth. Populations referred to in previous studies as *C. yaha* are reclassified as *C. tesay*; *C. yaha* is an endemic species of the neighboring Urugua-í stream known only from nine specimens because the species has not been collected since 1989 (when a dam was constructed on this stream). The taxonomic status of the populations referred to here as *C. iguassuensis* remain tentative because these form a separate clade in mtDNA analysis, reveal slight morphological differences, and have a wide distribution gap to the type locality with similar yet undescribed species in the intervening area.

Key words. Areas of endemism, morphoecological diversification, La Plata River basin, Paraná, species flocks.

INTRODUCTION

The Iguazú River is a large tributary of the Paraná River, which together with the Paraguay and Uruguay Rivers form one of the largest river systems in the World, the La Plata River basin. The Iguazú River is 1,320 km long, with a drainage basin of 72,000 km^2 in the states of Paraná and Santa Catarina in Southern Brazil, and in the Province of Misiones in Argentina (Maack, 2001; Abell *et al.*, 2008; FEOW). The Iguazú River originates at an altitude of 908 m in the Brazilian state of Paraná close to its capital Curitiba. The total descent of the river is 830 m to its confluence with the Paraná River at 78 m (Baumgartner *et al.*, 2012). The river is the southernmost large left-bank tributary of the Paraná flowing in a general east-west direction from close to the edge of the western slope of the Serra do Mar (Paiva, 1982). The Iguazú River basin has a humid subtropical mesothermal climate with hot summers and rainfall that is constant throughout the year (Hijmans *et al.*, 2004). The formation of the Iguazú River basin dates from the Cretaceous era (MINEROPAR, 2014) and was associated with the movements of uplift of the Serra do Mar due to rifting from Africa, giving rise to three plateaus: 1. region of Curitiba; 2. region of Ponta Grossa, and 3. region of Guarapuava (Maack, 2001). From these geomorphological features, the Iguazú River is naturally divided into three regions (Ingenito *et al.*, 2004; Baumgartner *et al.*, 2012): the upper, the middle, and the lower Iguazú.

The lower Iguazú River (subject of this study) is geologically distinct from the rest of the Iguazú basin by being composed of and having exposed at its surface volcanic flood basalts of the Paraná group whilst the upper and especially middle sections are predominantly of sedimentary rocks with a meandering character of the river (Maack, 1981; MINEROPAR, 2014). These flood basalts are part of the Paraná–Etendeka traps (the Etendeka plateau is in SW Angola and NW Namibia), one of the Large Igneous Provinces of our planet. The Paraná–Etendeka traps comprise a large igneous province shared between South America and Africa across the Atlantic Ocean, whose present distribution is a direct result of the rifting between South America and Africa during the early Cretaceous (128 to 138 Mya). The flood basalts are the reason why the lower Iguazú River (and other rivers of the southern region of the Brazilian shield on the Paraná traps) has a large number of rapids and waterfalls that arise as the products of crustal discontinuities between separate lava flows within the deforming rocks. The most significant waterfalls are: Salto Grande by the town of União da Vitória (13 m high, the upper border of the lower Iguazú), Salto Santiago (40 m), Salto Osório (30 m) and the 72 m high Iguazú Falls (Maack, 1981).

The Iguazú (meaning "big water" in the local Guarani language) Falls (Figure 1) form the lower border of the lower Iguazú and are the only large falls on the main Iguazú River channel which have not been flooded by hydroelectric dams. The falls separate a unique and highly endemic fauna in the Iguazú River from the rest of the Paraná River basin. Numerous islands along the 2.7-kilometres-long edge divide the falls into many separate waterfalls and cataracts varying between 30 to 72 meters in height. The number of these smaller waterfalls fluctuates from 150 to 300 depending on the water level. Approximately half of the river's flow falls through a high and narrow chasm called the Devil's Throat (Garganta del Diablo, Garganta do Diablo).

The Devil's Throat is U-shaped, 72 m high, 150 m wide and 700 m long. The Iguazú River is 1,200 m wide above the falls, then below the falls drops into a canyon of only 65-100 m width.

The ichthyofauna of the Iguazú River includes at present 106 described species (Baumgartner *et al.*, 2012). The level of endemism is very high, with about 70% of exclusive species (Baumgartner *et al.*, 2012). On the other hand the cichlid fish fauna of the Iguazú River is relatively poor, limited to three native genera (*Australoheros*, *Crenicichla*, and *Gymnogeophagus*), but notable for its interesting fauna of closely related, sympatric and diversified species of *Crenicichla* (Piálek *et al.*, 2012). All these genera are within the Iguazú River restricted to the lower Iguazú.

Crenicichla comprises at present 89 valid species (Froese and Pauly, 2015) but at least half as many are known and remain to be formally described (Artigas Azas, 1996-2014; Stawikowski and Werner, 2004) and many more are postulated based on DNA phylogeny (unpublished data) making *Crenicichla* the largest cichlid genus in the Neotropics. So far 18 species have been reported only from Argentina (Mirande and Koerber, 2015). *Crenicichla* is traditionally divided into five species groups (Ploeg, 1991; Stawikowski and Werner, 2004; Kullander *et al.*, 2010; Piálek *et al.*, 2012). The species groups were defined using external morphological characters (color patterns, meristic characters) and geographic distributions. The phylogenetic relationships within *Crenicichla* confirmed the monophyly of the species groups, however with the genus *Teleocichla* nested within *Crenicichla* (Piálek *et al.*, 2012; López-Fernández *et al.*, 2010; not resolved in Kullander *et al.*, 2010). The genus has a widespread distribution in South America east of the Andes. Most of the species groups of *Crenicichla* are largely sympatric (but not necessarily syntopic) with a distribution being centered in the Amazon and Orinoco drainages. One species group, the *C. lacustris* group is, however, allopatric, distributed in SE South America in the La Plata River basin (the Paraná and Uruguay Rivers) and in the Atlantic coastal drainages. It is the southernmost *Crenicichla* species group and also the southernmost cichlid group in South America.

The *Crenicichla lacustris* species group has a comparatively high diversity (Kullander *et al.*, 2010) and comprises two species complexes - *C. missioneira* and *C. mandelburgeri* - from the Paraná and Uruguay River basins, respectively (Lucena and Kullander, 1992;

Figure 1 - The 72 m high Iguazú Falls form the natural inferior limit of the lower Iguazú biogeographic area.

Piálek *et al.*, 2012). Each of these complexes shows a wide range of analogous head/mouth and coloration adaptations, yet the two complexes are each monophyletic and are not immediate sister groups, resulting in a striking case of parallel evolution in parallel river systems (Piálek *et al.*, 2012). The core of the diversity of the Paranean *C. mandelburgeri* species complex lies undoubtedly in the lower Iguazú River whose fauna includes all the four distinct ecomorphotypes (thick-lipped, long-headed-long-mouthed, short-mouthed; the latter form with either pointed or molariform pharyngeal teeth) in sympatry. The lower Iguazú species were however not resolved as a monophyletic lineage in a multilocus phylogenetic analysis of three mitochondrial (cyt*b*, ND2, 16S) and one nuclear marker (S7 intron 1) of Piálek *et al.* (2012).

The goal of this paper is to describe two new species of *Crenicichla* endemic to the lower Iguazú River and to revise the taxonomic status of their two congeners (*C. iguassuensis*, *C. tesay*). We also bring new and detailed information on the ecological differentiation of this sympatric quartet.

MATERIAL AND METHODS

Specimens for anatomical study were cleared and counterstained (c&s) following the method of Taylor and Van Dyke (1985). Measurements were taken as described by Kullander (1986) individually for *Crenicichla* and the pattern of their variation was visualized using principal component analysis (PCA) implemented in Canoco 5 (Microcomputer Power, Ithaca, NY, USA) according to Šmilauer and Lepš (2014). Counts were taken as in Kullander (1986). Pharyngeal teeth and frayed zone descriptions follow Casciotta and Arratia (1993). An asterisk denotes holotype values. Body length is expressed as standard length (SL). E1 scale counts refer to the scales in the row immediately dorsal to that containing the lower lateral line (Lucena and Kullander, 1992). Institutional abbreviations follow Ferraris (2007). Voucher specimens are deposited in the Museo Argentino de Ciencias Naturales (MACN), Museo de La Plata (MLP), and Asociación Ictiológica (AI).

RESULTS

The *Crenicichla* fauna of the lower Iguazú River includes based on our results four endemic species, and another additional species (*C. lepidota*) that is not endemic to the river and belongs to the *C. saxatilis* species group and is thus only very distantly related to the remaining species which belong to the *C. lacustris* species group. The four species within the lower Iguazú are *C. iguassuensis*, *C. tesay*, and the two new species described herein and previously referred to as *Crenicichla* sp. 'Iguazú biglips 2' and *C.* aff. *yaha* 'Iguazú 1' (Piálek *et al.*, 2012).

Taxonomy

Family Cichlidae Bonaparte, 1835
Genus *Crenicichla* Heckel, 1840

***Crenicichla tuca*, new species** (Figures 2A; 3B; 4A, B; 5; Table 1)
Crenicichla sp. ´Iguazú biglips 2´—Piálek *et al.* 2012
Holotype. Male, MLP 10818 (ex MACN-ict 9522), DNA165, 1 ex, 150.3 mm SL, ARGENTINA, Misiones Province, lower Iguazú River above Iguazú Falls, arroyo Deseado, 25°40'11.7" S 53°55'59.5"W, May 2010, Piálek *et al.* (Figure 2A).

Paratypes. All from ARGENTINA, Misiones Province, lower Iguazú River basin above Iguazú Falls. MLP 10817 (ex MACN-ict 9523), DNA188, 1 ex, 124.1 mm SL, Iguazú main channel, 25°37'19.5"S 54°05'40.5"W, May 2010, Piálek *et al*. MLP10819, DNA280/281/282, 3 ex, 86.0-117.2 mm SL, at the mouth of arroyo Ñandú, Parque Nacional Iguazú, 25°42'11.7"S 54°25'31.2"W, Feb 2012, Casciotta *et al.* MLP 10821, (ex CIES 65) 1 ex., (c&s) 140.0 mm SL.

Etymology. The specific epithet tuca is a Guaraní word (tucá) meaning toucan (*Ramphastos*) in reference to the similarly enlarged lips/beak.

Diagnosis. *Crenicichla tuca* sp. n. is distinguished from all other *Crenicichla* species by hypertrophied upper and lower lips on large jaws in combination with presence of 1 or 2 dark rectangular unocellated blotches below upper lateral line just behind posterior margin of opercle.

Crenicichla tuca additionally differs from all other Iguazú congeners in having a longer head (Table 1), yellow-orange ground coloration with large orange dots on the cheek and opercular series in both sexes in adult specimens, the suborbital stripe reduced and decomposed into a few widely separated dots.

Furthermore, *C. tuca* is distinguished from C. *iguassuensis* by a deeper head and

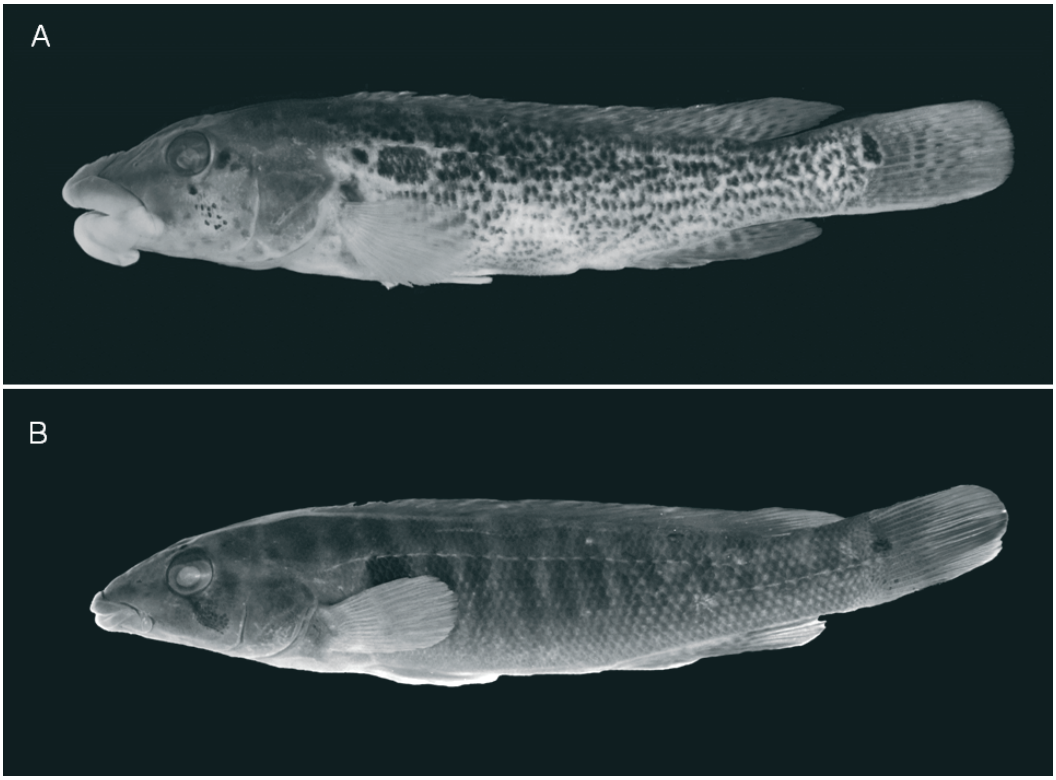

Figure 2 - Holotypes of the two newly described species from the lower Iguazú River.. (A) *C. tuca* sp. n., holotype, male, MLP 10818 (ex MACN-ict 9522), DNA165, 150.3 mm SL. (B) *C. tapii* sp. n., holotype, female, MLP 10560, DNA 283, 105.4 mm SL.

an isognathous or hypognathous mouth, from *C. tapii* sp. n. by a shorter caudal peduncle and a longer interorbital width, and from *C. tapii* sp. n. and *C. tesay* by longer upper and lower jaws (Table 1).

Description. Morphometry is given in Table 1. Morphometric comparisons are made within the lower Iguazú endemic species. Head length and snout length were taken including the hypertrophied upper lip. Body elongate, depth 4.4 to 4.7 times in SL. Head rather large, deeper than wide. Mouth rather large, narrow, upper and lower jaws long. Oral jaws isognathous (3) or upper jaw slightly longer (mouth hypognathous; 3). Upper and lower lip hypertrophied, lower lip fold not interrupted

Table 1 - Proportional measurements in percents of standard length of 87 specimens of the lower Iguazú *Crenicichla* species including holotypes of two newly described taxa. SD=standard deviation.

	C. tuca		***C. tapii***		***C. iguassuensis***	***C. tesay***
	n = 5		n = 29		n = 30	n = 23
	holotype	**mean ± SD**	**holotype**	**mean ± SD**	**mean ± SD**	**mean ± SD**
		range		*range*	*range*	*range*
standard length [mm]	150.3		105.4			
head length	35.7	**34.8 ± 0.77**	28.4	**28.6 ± 1.09**	**33.0 ± 0.85**	**31.6 ± 1.24**
		33.6–35.7		*26.7–30.8*	*31.0–34.4*	*29.4–34.0*
snout length	16.2	**15.3 ± 0.75**	11.4	**11.2 ± 0.90**	**11.9 ± 1.00**	**12.6 ± 1.14**
		14.4–16.2		*9.4–12.9*	*10.3–14.4*	*11.2–14.7*
orbital diameter	6.3	**6.9 ± 0.40**	6.5	**6.6 ± 0.30**	**6.7 ± 0.71**	**7.1 ± 0.49**
		6.3–7.2		*6.00–7.29*	*5.3–8.7*	*6.1–8.6*
upper jaw length	15.4	**14.8 ± 0.92**	9.4	**9.1 ± 0.57**	**12.7 ± 1.08**	**10.9 ± 0.81**
		13.5–15.6		*7.8–10.5*	*10.5–15.6*	*9.3–12.3*
lower jaw length	17.8	**16.4 ± 1.07**	10.8	**11.0 ± 0.71**	**15.9 ± 1.10**	**12.4 ± 0.68**
		15.2–17.8		*9.2–12.5*	*12.3–18.3*	*11.3–13.6*
interorbital width	8.3	**6.9 ± 0.86**	5.5	**5.7 ± 0.42**	**6.4 ± 0.64**	**7.2 ± 0.61**
		6.0–8.3		*4.9–6.6*	*5.5–8.0*	*6.1–8.6*
head depth	18.8	**18.1 ± 0.62**	15.8	**16.3 ± 0.78**	**15.3 ± 1.06**	**18.2 ± 1.15**
		17.4–18.8		*15.2–18.0*	*13.5–17.2*	*16.4–19.9*
body depth	21.9	**22.1 ± 0.67**	21.7	**22.2 ± 1.13**	**19.4 ± 0.99**	**23.4 ± 1.22**
		21.2–23.0		*20.3–25.8*	*17.4–21.9*	*20.9–25.9*
pectoral-fin length	18.2	**20.1 ± 1.3**	18.7	**20.2 ± 0.74**	**18.9 ± 0.92**	**20.9 ± 0.89**
		18.2–21.6		*18.7–21.3*	*17.1–20.6*	*19.6–22.9*
length of last dorsal-fin spine	12.1	**12.7 ± 0.60**	14.1	**14.6 ± 1.19**	**11.1 ± 1.14**	**13.3 ± 1.05**
		12.0–13.4		*12.0–16.5*	*8.9–13.4*	*10.6–15.1*
caudal-peduncle depth	10.5	**11.0 ± 0.45**	11	**11.4 ± 0.29**	**10.1 ± 0.46**	**11.5 ± 0.41**
		10.5–11.4		*10.8–11.9*	*9.2–11.0*	*10.7–12.5*
caudal-peduncle length	16.6	**16.3 ± 0.65**	18.8	**18.9 ± 0.66**	**16.3 ± 0.75**	**16.9 ± 0.61**
		15.1–16.6		*17.5–20.4*	*14.8–17.7*	*15.5–18.1*

medially. Nostrils dorsolateral, equidistant between anterior margin of orbit and snout tip. Posterior margin of preopercle serrated. Scales on flank strongly ctenoid. Head scales cycloid. Predorsal scales small, superficially embedded in skin. Interopercle naked. Cheek scaled, 6 to 9 scales below eye embedded in skin, 6(1), 7(1), 8(3*). Scales in E1 row 52(1), 53(1), 56(1), 58(2*). Scales in transverse row 12/13 (1), 12/14 (2*), 12/15 (2). Scale rows between lateral lines 2(4*) or 3(1). Upper lateral line scales 23(5*). Lower lateral line scales + pored scales on caudal fin: 11+2(2), 12+2(2*), 13+3(1). Dorsal, anal, pectoral and pelvic fins naked. Dorsal fin XX,10(1*); XX,11(1); XX,12(3). Anal fin III,8 (2); III,9(3*). Pectoral fin 16(4*), 17(1). Caudal-fin squamation not reaching (5) half of fin length at level of medial fin-rays, reaching (1). Soft-dorsal fin rounded or pointed, extending to caudal-fin base. Tip of anal fin reaching (1) or not (5) caudal-fin base. Caudal fin slightly rounded. Pectoral fin rounded, not reaching the tip of pelvic fin. Microbranchiospines absent on 2nd to 4th gill arches (1 c&s). Gill rakers externally on 1st gill arch: 3 on epibranchial, 1 on angle, and 9 on ceratobranchial (1 c&s). Presence of patches of unicuspidate teeth on 4th ceratobranchial (1 c&s). Lower pharyngeal tooth plate relatively gracile with numerous small unicuspid, and bicuspid crenulated anteri-

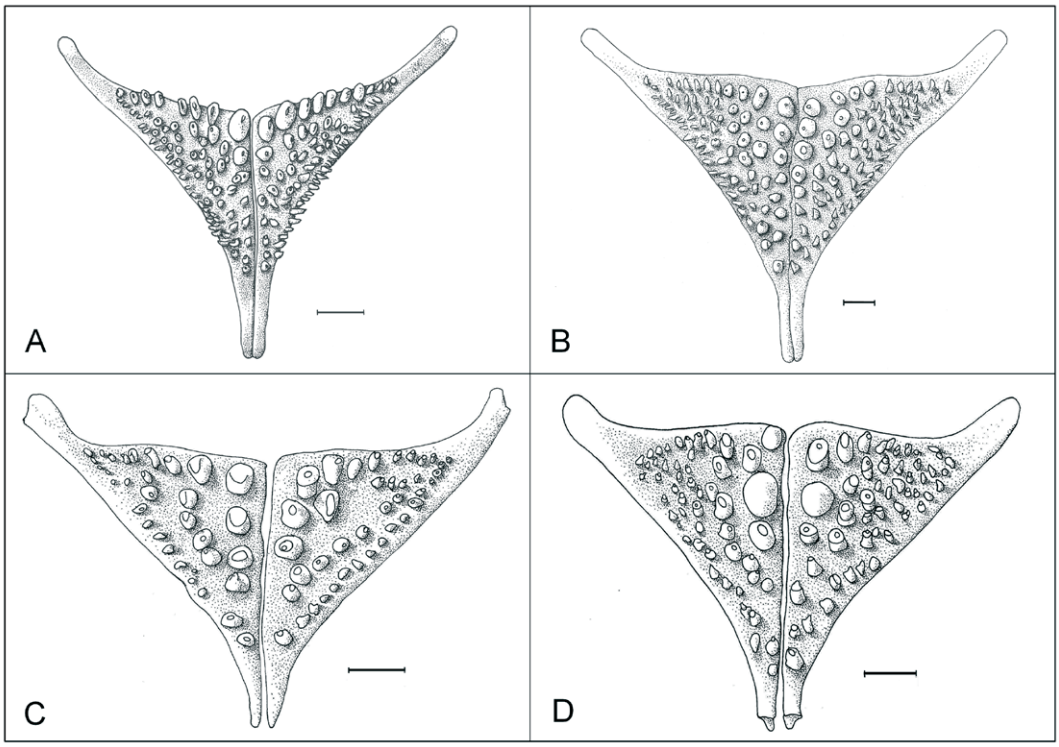

Figure 3 - Lower pharyngeal tooth plates of the four sympatric species from the lower Iguazú River (occlusal view, scale bar 1 mm). (A) *C. iguassuensis*, AI 215, 69.0 mm SL. (B) *C. tuca* sp. n., MLP 10821, 140.0 mm SL. (C) *C. tapii* sp. n., MLP 10805, 94.4 mm SL. (D) *C. tesay*, MLP 10825, 77.6 mm SL. Species differ both in the shape and massiveness of the tooth plate and in the tooth morphology – note the increasing robustness of the tooth plate and teeth from the piscivorous *C. iguassuensis* to the molluscivorous *C. tesay*.

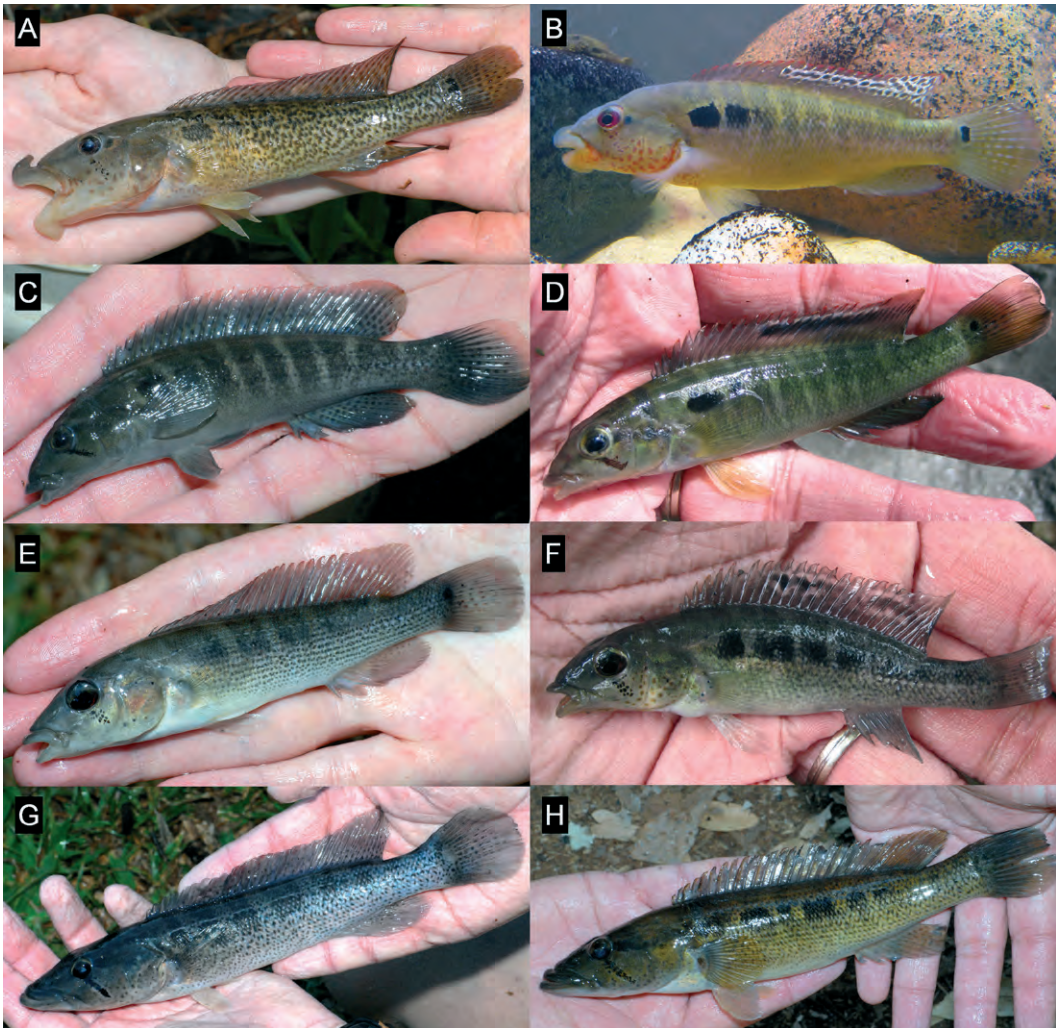

Figure 4 - Alive specimens of the four sympatric species from the lower Iguazú River. (A,B) *Crenicichla tuca* sp. n. (A, male; B, female – photo by Ariel Puentes). Note lack of body spotting in females as in *C. tapii* contrasting to spotting in both sexes of *C. iguassuensis* and *C. tesay*. (C,D) *Crenicichla tapii* sp. n. (C, male; D, female). Note sexual coloration dimorphism in background body coloration similar to *C. yaha* and *C. iguassuensis*. Note different body coloration, vertical double-bars, lack of spotting on head and body, narrow and well formed suborbital stripe, small mouth and head and absence of thick lips distinguishing it from *C. tuca* sp. n. Note additionally the suborbital stripe which in combination with the vertical double-bars and lack of dots on body distinguishes it readily from the similarly small-headed *C. tesay*. (E,F) *Crenicichla tesay* (E, male; F, female in preparation for breeding; note short jaws, small mouth and head and different suborbital stripe compared to the otherwise similar *C. iguassuensis*). (G,H) *Crenicichla iguassuensis* (G, male; H, non-breeding female).

orly curved teeth, those along suture relatively enlarged (Figure 3B). Upper pharyngeal tooth plate with unicuspidate and bicuspid crenulated teeth, few of them rather large. Frashed zone bearing one concavity with small unicuspid teeth (1 c&s). Premaxillary ascending process longer than dentigerous one. Premaxilla with 21 unicuspid

teeth on outer row, larger than inner ones. 6 tooth rows near symphysis. Dentary with 2 unicuspid teeth on outer row, 4 rows near symphysis. Premaxillary and dentary outer row teeth slightly movable, inner ones fully depressible. Total vertebrae: 35 (1 c&s).

Coloration in life. One or two dark conspicuous rectangular blotches below upper lateral line immediately behind posterior opercular margin. Orange dots on cheek and lower opercular series. Flanks without distinct vertical bars. Small black subcircular spot, well separated from base of fin, just above of midline of caudal fin. Preorbital stripe, between snout tip and anterior margin of orbit, faint gray. Postorbital stripe gray, usually reaching preopercle distal margin; darker close to the posterior margin of orbits. Suborbital stripe decomposed into a few widely separated dots or nearly absent in some specimens. Background of lower body grayish-yellow to bright yellow-orange, dorsum and dorsal portion of head olive to grey. Adult ripe specimens with a yellow-orange branchiostegal membrane. Breeding females with the posterior ¾ of the dorsal fin with a black longitudinal stripe (or decomposed into spots) limited below and above by a white stripe (Figure 4B). Males with numerous dark scattered dots on body, the caudal peduncle and on unpaired fins, females without. *Crenicichla tuca* has the most pronounced sexual dimorphism in body spotting among the four endemic Iguazú *Crenicichla* species.

Coloration in alcohol. Melanistic coloration as in life. Background of body pale gray. The diagnostic dots on cheek and lower opercular series very pale to absent. Flanks with numerous irregular dark dots in males, sometimes arranged in narrow horizontal lines. Unpaired fins smoky with dark dots in males. Pectoral and pelvic fins pale yellow.

Figure 5 - Different views on a head of *C. tuca* sp. n. – paratype from the main channel of Iguazú MLP 10817 (ex MACN-ict 9523).

Distribution. *Crenicichla tuca* sp. n. is endemic to the lower Iguazú River basin above the Iguazú Falls and is found predominantly in the main channel of the river but also in large tributaries (i.e. Deseado and San Antonio Rivers in the Misiones Province, Argentina). It is absent from small tributaries, especially those without rocky bottoms. The species distribution extends upstream of the Misiones Province, Argentina into the neighboring state of Paraná, Brazil (see *Crenicichla* sp. "IGUAÇU" in Varella, 2011).

Habitat. *Crenicichla tuca* sp. n. was captured only rarely, always as single specimens. All specimens except two were caught in the main channel of the Iguazú River. Some of the largest specimens were caught using hook-and-line. In the main channel specimens were observed only as single individuals among the rocks from the walkways over the river ramming their heads and thick lips against the rock surfaces. Field observations, stomach contents and head and lip morphology suggest a similar diet as in the same ecomorph (*Crenicichla tendybaguassu*) in the *C. missioneira* species complex from the Uruguay River basin (Burress *et al*., 2013). Ariel Puentes (pers. com.) observed a captive aquarium specimen digging with half-submerged head in the sandy bottom.

***Crenicichla tapii*, new species** (Figures 2B; 3C; 4C, D; 6; Table 1)
Crenicichla aff. *yaha* ´Iguazú 1´—Piálek *et al.* 2012

Holotype. Female, MLP 10560, DNA283, 105.4 mm, ARGENTINA, Misiones Province, lower Iguazú River above Iguazú Falls, at the mouth of arroyo Ñandú, Parque Nacional Iguazú, 25°42'11.7"S 54°25'31.2"W, Feb 2012, Casciotta *et al.* (Figure 2B).
Paratypes. All from ARGENTINA, Misiones Province, lower Iguazú River basin above Iguazú Falls. MLP 10561, 20 ex., 78.3-117.5 mm, collected with the holotype. MLP10804, 10 ex., 62.3- 120.3 mm, at the mouth of arroyo Ñandú, Parque Nacional Iguazú, 25°42'11.7"S 54°25'31.2"W, Feb 2012, Casciotta *et al*. MLP10805 (ex AI 307), 2 c&s ex., 76.0-94.4 mm, collected with the holotype. MACN-ict 9553, 2 ex., 86.0-111.0 mm, arroyo Deseado, 25°40'11.7"S 53°55'59.5"W, Nov 2007, Říčan *et al*.

Etymology. The specific epithet tapii is a Guaraní word (tapií) meaning tapir (*Tapirus*) in reference to the subterminal mouth and the concave head of the species associated with its grazing semi-herbivorous mode of feeding similar to that of the tapir but highly untypical for the generally predatory *Crenicichla*.

Diagnosis. *Crenicichla tapii* sp. n. is distinguished from all other *Crenicichla* species by a small and narrow isognathous or hypognathous mouth in combination with a well-formed narrow suborbital stripe, and the presence of 1 or 2 dark rectangular blotches below the upper lateral line in the 1st vertical flank stripe.

Crenicichla tapii additionally differs from all other Iguazú congeners in well-developed vertical double-bars, a short head and interorbital distance and a longer caudal peduncle (Table 1).

Furthermore, *C. tapii* differs from *C. tesay* in having a very narrow more posteriorly inclined usually not into spots decomposed suborbital stripe and in absence of dark narrow horizontal dotted stripes or scattered dots on flanks. *Crenicichla tapii* further differs from *C. tuca* sp. n. and *C. iguassuen-*

sis in short upper and lower jaws (Table 1) and from *C. tuca* sp. n. in the absence of hypertrophied lips.

Description. Morphometry is given in Table 1. Morphometric comparisons are made within the lower Iguazú endemic species. Body elongate, depth 3.9 to 4.9 times in SL. Head small, deeper than wide. Mouth small and narrow, jaws short. Oral jaws isognathous (8) or upper jaw slightly longer (mouth hypognathous; 6). Tip of maxilla not reaching anterior margin of orbit. Lower lip fold widely interrupted medially. Nostrils nearer to the anterior margin of orbit than to the snout tip. Posterior margin of preopercle usually serrated (27) or not serrated (7). Scales on flank strongly ctenoid. Head scales cycloid. Predorsal scales small, superficially embedded in skin. Interopercle naked. Cheek scaled, 6 to 10 scales below eye embedded in skin, 6 (1), 7 (1), 8(19*), 9(10), 10(1). Scales in E1 row 53(1), 54(4), 55(3), 56(6), 57(8), 58(2), 59(2), 60(6*), 62(1), 63(1). Scales in transverse row 10/14(3), 10/15(1), 10/16(1), 11/13(3), 11/14(6), 11/15(7), 11/16 (5), 12/14 (1), 12/15 (1*), 12/16 (3), 12/18 (1), 13/14 (1), 13/17 (1). Scale rows between lateral lines 2(24) or 3(4). Upper lateral line scales 20(1), 24 (1), 25(4), 26(6), 27(7), 28(7), 29(7*), 30(1). Lower lateral line scales + pored scales on caudal fin: 8+1(3), 8+2(4), 9+1(3), 9+2(6), 9+3(1), 10+1(4), 10+2(4), 10+3(1), 11+1(1), 11+2(5*), 12+2(1), 13+2(1). Dorsal, anal, pectoral and pelvic fins naked. Dorsal fin XX,12(2); XXI,10(1); XXI,11(12*); XXI,12(6); XXI,13(1); XXII,10(3); XXII,11(6); XXII,12(1); XXIII,11(1). Anal fin III,8 (6); III,9(25*); III,10(3). Pectoral fin 15(2), 16(32*). Caudal-fin squamation not reaching half of fin length at level of medial fin-rays. Soft-dorsal fin rounded or pointed, extending to caudal-fin base. Tip of anal fin not reaching caudal-fin base. Caudal fin slightly rounded. Pectoral fin rounded, not reaching the tip of pelvic fin. Microbranchiospines not observed on 2nd to 4th gill arches (2 c&s). Gill rakers externally on 1st gill arch: 2 on epibranchial, 1 on angle, and 8 on ceratobranchial (2 c&s). Absence of patches of unicuspidate teeth on 4th ceratobranchial (2 c&s). Lower pharyngeal tooth plate rather robust with unicuspid, and bicuspid crenulated curved anteriorly teeth, midlateral teeth along the suture and posterior teeth enlarged, unicuspid or molarized (Figure 3C). Upper pharyngeal tooth plate with unicuspidate and bicuspid crenulated teeth. Frashed zone bearing one concavity with small unicuspid teeth (2 c&s). Premaxillary ascending process longer than dentigerous one. Premaxilla with 15-16 (5) unicuspid teeth on outer row, larger than inner ones. Four to 5 tooth rows near symphysis. Dentary with 17 to 22 (5) unicuspid teeth on outer row, 4 to 5 rows near symphysis forming a scraping-pad. Premaxillary and dentary outer row teeth slightly movable, inner ones fully depressible. Total vertebrae: 37 (2 c&s).

Coloration in life. One or two prominent black blotches on body below upper lateral line in the first vertical double-bar behind head. Flanks with 8 to 9 narrow black vertical double-bars reaching onto belly. Two additional bars on caudal peduncle. Small black subcircular spot, well separated from base of fin, just above of midline of caudal fin. Juveniles with about 5 dark blotches just below upper lateral line. Preorbital stripe, between snout tip and anterior margin of orbit, faint gray. Postorbital stripe gray, usually not reaching preopercle distal margin. Suborbital stripe black, compact, narrow (26; rarely fragmented, 4), reaching (17) or not (13) ventral margin of cheek.

Background of body greenish to yellow-green (without any dots on body and fins) in adult females, darker blue-green to grey in adult males (with dotted unpaired fins and dotted caudal peduncle). *Crenicichla tapii* has the most pronounced sexual dimorphism in background body coloration among the four endemic Iguazú *Crenicichla* species. Smaller specimens (below 50 mm SL) yellow-green, yellow, or golden. Adult ripe specimens with a yellow-orange branchiostegal membrane. Adult females in breeding condition with a golden to reddish band along mid-body below the midlateral blotches and dorsal fin with a black band along posterior ¾ of dorsal portion of dorsal fin with a white margin encircling the black band (Figures 4D; 6). Branchiostegal membrane in breeding females distinctly yellow-orange. Males with numerous dark scattered dots in unpaired fins and on the caudal peduncle, females without.

Coloration in alcohol. Melanistic coloration as in life. Background of body pale gray to dark grey in large specimens, smaller ones (46.7–63.0 mm SL) pale gray. Dorsal, anal, pelvic, and caudal fins dark gray. Pectoral fin pale yellow. Females with dorsal, anal, and caudal fins dark gray.

Distribution. *Crenicichla tapii* sp. n. is endemic to the lower Iguazú River basin above the Iguazú Falls and is found predominantly in the main channel of the river but also in large tributaries (i.e. Deseado stream in the Misiones Province, Argentina). It is absent from small tributaries, especially those without rocky bottoms. The species distribution extends upstream of the Misiones Province, Argentina into the neighboring state of Paraná, Brazil (see *Crenicichla* sp. "IGUAÇU" in Varella, 2011).

Habitat. *Crenicichla tapii* sp. n. is relatively common only in the main channel of the Iguazú River (Figure 7), it is uncommon in lower reaches of large tributaries (e.g. Deseado stream) and absent from small tributaries in Argentina. In the main channel specimens can be observed in schools

Figure 6 - School of *C. tapii* sp. n. (A) Note gregarious foraging and also the breeding coloration of the dominant female (photo by Jan Štefka). (B) Detail of a different specimen of female in breeding coloration.

on the flat-rock substrate from the walkways over the river grazing on periphyton (Figure 6). *Crenicichla tapii* sp. n. was always captured only in direct association with flat slab-like exposed rocky bottoms with epiphyte growths, never above gravel or soft sediment-covered bottoms. All specimens were caught only with gill-nets, never with baited hook-and-line (as in *C. tuca*). Field observations, stomach contents and head morphology confirm that it is a periphyton-grazing species requiring exposed rocky bottoms and clear water enabling the growth of periphyton.

Figure 7 - (A) The main Iguazú River channel just above the Iguazú Falls. In this area all the four species live in sympatry and can be even observed during low water conditions by visitors of the Iguazú National Park from the footbridge to the Devil's Throat (B).

***Crenicichla iguassuensis*, Haseman 1911**
(Figures 3A; 4G, H; Table 1)
Crenicichla tesay—Casciotta *et al*. 2013
Crenicichla tesay—Piálek *et al.* 2012
Crenicichla tesay—Casciotta *et al*. 2010
Crenicichla tesay—Piálek *et al*. 2010

Description. Morphometry is given in Table 1. Morphometric comparisons are made within the lower Iguazú endemic species. Body long and slender, depth 4.6 to 5.7 times in SL. Head rather large, deeper than wide. Mouth large, wide, lower jaw long and distinctly prognathous. Nostrils dorsolateral, equidistant between anterior margin of orbit and snout tip. Posterior margin of preopercle serrated. Scales on flank ctenoid. Head scales cycloid. Predorsal scales small, superficially embedded in skin. Cheeks scaled, 6 to 9 scale rows below eye embedded in skin. Scales in E1 row 58(4), 61(1), 62(1), 63(2), 64(1), 65(7), 66(2), 67(4), 68(2), 69(5), 70(1). Scales in transverse row 11/13(1), 11/14(4), 11/15(5), 11/16(4), 12/14(2), 12/15(4), 12/16(6), 12/17(2), 13/14(1), 14/15(1). Three scale rows between lateral lines. Upper lateral line scales slightly larger than the adjacent scales with 23(6), 24(3), 25(7), 26(9), 27(3), 28(1), 29(1) scales. Lower lateral line scales equal in size to adjacent ones with 11(1), 12(5), 13(9), 14(9), 15(4), 16(2) scales. Dorsal, anal, pectoral and pelvic fins naked. Dorsal fin XXI,11(1); XXI,12(7); XXI,13(3); XXII,11(4); XXII,12(11); XXII,13(3); XXIII,12(1). Anal fin III,9(13); III,10(16); III,11(1). Pectoral fin 16(4), 17(22), 18(4). Lower pharyngeal tooth plate gracile and slender with numerous small unicuspid, and bicuspid crenulated anteriorly curved teeth, those along posterior edge relatively enlarged (Figure 3A).

Coloration in life. Body with about 6 midlateral blotches along body axis, the same number of faint wide vertical bars on dorsal part of body. Body densely dotted with small irregular black dots. Two additional bars on caudal peduncle. Small indistinct black subcircular spot, well separated from base of fin, just above of midline of caudal fin. Juveniles also with about 6 dark blotches just below upper lateral line, less spotted. Preorbital stripe, between snout tip and anterior margin of orbit, faint gray. Postorbital stripe gray to black. Suborbital stripe dominant, black, compact, long and narrow, distally pointed, reaching ventral margin of cheek. Background of body grey (usually males) or greenish to yellowish (usually females). Adult females in breeding condition with a dorsal fin with a black band along posterior ¾ of dorsal portion of dorsal fin with a white margin encircling the black band. Both sexes have thoroughly dotted body, males also unpaired fins.

Coloration in alcohol. Melanistic coloration as in live, background of body pale gray to dark grey.

Distribution. *Crenicichla iguassuensis* is endemic to the lower Iguazú River basin above the Iguazú Falls. The species distribution extends upstream from the Misiones Province, Argentina into the neighboring state of Paraná, Brazil (see Varella, 2011).

Habitat. *Crenicichla iguassuensis* is a common and dominant *Crenicichla* species in the lower Iguazú River basin (together with *C. tesay*), both in the main channel as well as in all tributaries. *Crenicichla iguassuensis* was captured above all kinds of bottoms including flat slab-like exposed rocky bottoms, gravel or soft sediment-covered bottoms. Field observations, stomach contents and head and pharyngeal tooth mor-

phology all suggest that it is a piscivorous species (Figures 3A; 4G, H).

Remarks. *Crenicichla iguassuensis* Haseman 1911 was described from the Rio Iguazú at Porto União da Victoria, Paraná, Brazil at the limit between the lower and the middle Iguazú River. This locality is 280 air km (but 530 river km including several previously existing major waterfalls) of distance and 530 m of altitude difference (745 vs. 215 m a.s.l.) from the here studied populations in the lower Iguazú. The type locality is within the Araucaria moist forests terrestrial ecoregion while the here studied populations in the lower Iguazú are from within the Alto Paraná Atlantic forests ecoregion which differ markedly in their climate and general biodiversity features.

We provisionally treat the large-mouthed populations with prognathous lower jaw from the studied areas in lower Iguazú in Argentina as synonymous with *C. iguassuensis*. Piálek *et al.* (2012) have referred them previously incorrectly as *Crenicichla tesay* based on morphological determination by JC (comparing them with the type collection of *C. tesay* that erroneously comprises also two specimens of the large-mouthed prognathous form, see further), and the fact that the molecular phylogeny of Piálek *et al.* (2012) places the Argentinean samples as a separate clade from *C. iguassuensis* specimen (GenBank Accession No. GQ199954) from the study of Kullander *et al.* (2010). The Argentinean populations may indeed be a distinct species (but not *C. tesay*; see below) from *C. iguassuensis* but the lack of fresh material (both for morphological and molecular analyses) of *C. iguassuensis* from the type locality precludes any final decision to the taxonomical question at hand.

***Crenicichla tesay*, Casciotta and Almirón 2008** (Figures 3D; 4E, F; Table 1)
Crenicichla yaha—Casciotta *et al*. 2013
Crenicichla aff. *yaha* ´Iguazú 2´—Piálek *et al.* 2012
Crenicichla yaha—Casciotta *et al*. 2010
Crenicichla yaha—Piálek *et al*. 2010

Description. Morphometry is given in Table 1. Morphometric comparisons are made within the lower Iguazú endemic species. Body elongate, depth 3.8 to 4.8 times in SL. Head rather small, deeper than wide. Mouth small, isognathous or hypognathous. Nostrils dorsolateral, equidistant between anterior margin of orbit and snout tip. Posterior margin of preopercle serrated. Scales on flank ctenoid. Head scales cycloid. Predorsal scales small, superficially embedded in skin. Cheeks scaled, 5 to 7 scale rows below eye embedded in skin. Scales in E1 row 49(1), 50(1), 52(4), 53(3), 54(10), 55(3), 56(5), 57(2), 58(2), 59(1). Scales in transverse row 10/14(3), 10/15(1), 11/13(4), 11/14(9), 11/15(3), 11/16(4), 12/13(2), 12/14(3), 12/15(1), 13/13(1), 15/13(1). Three scale rows between lateral lines. Upper lateral line scales slightly larger than the adjacent scales with 23(3), 24(11), 25(13), 26(5) scales. Lower lateral line scales equal in size to adjacent ones with 9(1), 10(1), 11(6), 12(9), 13(11), 14(4) scales. Dorsal, anal, pectoral and pelvic fins naked. Dorsal fin XX,11(3); XX,12(2); XXI,10(3); XXI,11(16); XXI,12(5); XXII,10(1); XXII,11(2). Anal fin III,6(1); III,8(10); III,9(19); III,10(2). Pectoral fin 16(28), 17(4). Lower pharyngeal tooth plate massive with several molariform teeth along the suture and the posterior edge (Figure 3D).

Coloration in life. Coloration virtually identical to *C. iguassuensis* except for suborbital stripe. Body with about 6 midlateral

blotches along body axis, the same number of faint wide vertical bars on dorsal part of body. Body thoroughly dotted with small irregular black dots. Two additional bars on caudal peduncle. Small indistinct black subcircular spot, well separated from base of fin, just above of midline of caudal fin. Juveniles also with about 6 dark blotches just below upper lateral line, less spotted. Preorbital stripe, between snout tip and anterior margin of orbit, faint gray. Postorbital stripe gray to black. Suborbital stripe wide (distally widened) and rather short, usually quite decomposed into separate black dots, not reaching ventral margin of cheek. Background of body grey (usually males) or greenish to yellowish (usually females). Adult females in breeding condition with a dorsal fin with a black band along posterior ¾ of dorsal portion of dorsal fin with a white margin encircling the black band (Figure 4F). Both sexes have thoroughly dotted bodies, males also dotted unpaired fins.

Coloration in alcohol. Melanistic coloration as in life, background of body pale gray to dark grey.

Distribution. *Crenicichla tesay* is endemic to the lower Iguazú River basin above the Iguazú Falls. The species distribution extends upstream of the Misiones Province, Argentina into the neighboring state of Paraná, Brazil (see *Crenicichla yaha* in Varella, 2011).

Habitat. *Crenicichla tesay* is a common and dominant *Crenicichla* species in the lower Iguazú River basin (together with *C. iguassuensis*), both in the main channel as well as in all tributaries. *Crenicichla tesay* was captured above all kinds of bottoms including flat slab-like exposed rocky bottoms, gravel or soft sediment-covered bottoms. Field observations, stomach contents and head and pharyngeal tooth morphology confirm that it is a picker with a substantial amount of hard-shelled molluscs in its diet.

Remarks. Casciotta and Almirón (2008) described *C. tesay* as a second species of *Crenicichla* (after *C. iguassuensis*) from the Iguazú River within the *C. lacustris* species group. The authors intended to describe the populations from the lower Iguazú in Argentina as a separate species from the geographically distant *C. iguassuensis* (see above). We have however in field expeditions noted that there is not one but two species in the lower Iguazú in Argentina that share the same coloration pattern (similar to *C. iguassuensis*) but that they differ in head and jaw morphology. Upon examination of the type series of *C. tesay* we have found that it is formed by both of these species with the holotype being of the small-mouthed form. The large-mouthed species is provisionally classified by us as *C. iguassuensis* as mentioned above. Before this confusion was realized the small-mouthed *Crenicichla* from the Iguazú has been called *C.* aff. *yaha* ´Iguazú 2´ (Piálek *et al*., 2012) or *C. yaha* (Casciotta *et al*., 2013; Varella, 2011), which is however a species described from the neighboring Urugua-í stream and which differs from *C. tesay* and Argentinean *C. iguassuensis* by not having a spotted body in neither sex (spotted in both sexes of *C. tesay* and *C. iguassuensis* in Argentina, but females in the type series of *C. iguassuensis* are likely unspotted – this requires verification in fresh material that is so far unavailable). As in the case of *C. tesay* the type series of *C. yaha* includes two species because one of the ten specimens is from the Iguazú River and represents probably *C. tesay* (not *C. yaha*); the determination of

the specimen from the Iguazú River is additionally complicated by the fact that the spotting (as the main diagnostic character) is not preserved in the specimen because it was for a long time exposed to sun-light during storage. *Crenicichla yaha* as here understood is thus endemic to the Urugua-í River and has unfortunately not been seen since the construction of the Urugua-í dam in 1989 (just prior to which the type series was collected) despite many collecting trips to the Urugua-í River stream by our team between 2007-2014. Seven of the nine known specimens including the holotype of *C. yaha* have been collected at a single locality within the Urugua-í River and this locality is now destroyed by the artificial lake formed by the hydroelectric dam.

In the original descriptions of *C. tesay* (Casciotta and Almirón 2008) the lower pharyngeal tooth plate was taken from a specimen of *C. iguassuensis* (caused by mixing the two species in the type series). Specimens of *C. tesay* (Figure 3D) have a robust

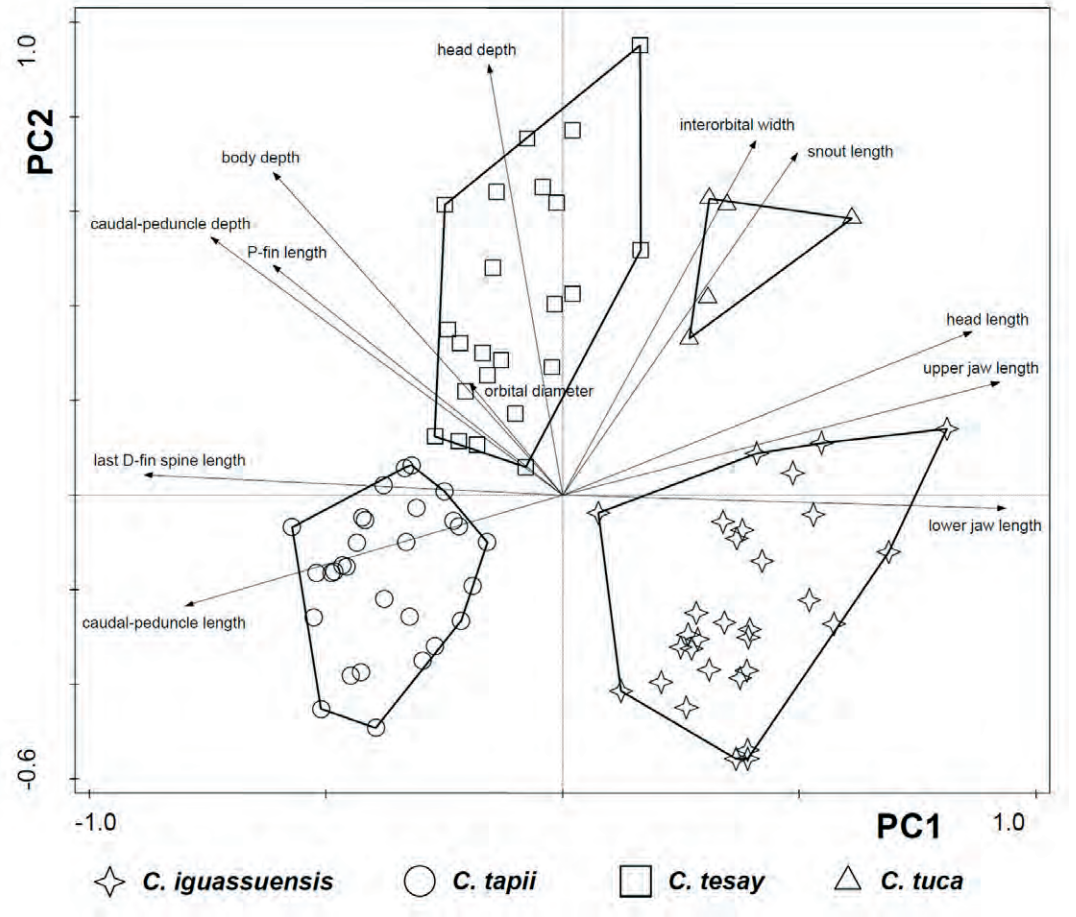

Figure 8 - Morphometric variation and discrimination of the four sympatric species from the lower Iguazú River analyzed by PCA. Morphological measurements (Table 1) of 87 specimens (above 80 mm SL) measured following Kullander´s (1986) methodology for *Crenicichla* were taken as proportional values in % of SL.

to very robust lower pharyngeal tooth plate with molariform teeth along the suture and along posterior edge suggesting a molluscivorous diet, which is also confirmed by stomach content observations.

PCA of morphometric data

The PCA scatter plot indicates that the four Iguazú species can be differentiated based purely on morphological measurements (Figure 8). Representing four diversified ecomorphs the four species occupy distinct quadrants in the morphological space. PC1 and PC2 explain 47.26 % and 26.65 % of the total variation, respectively.

DISCUSSION

Casciotta *et al.* (2006, 2010, 2013) and Piálek *et al.* (2010, 2012) have documented that the lower/middle Paraná-Iguazú basins host a very diverse fauna of *Crenicichla*, comparable to the only known diversified *Crenicichla* fauna in the neighboring Uruguay river basin (Lucena and Kullander, 1992; Lucena, 2007; Piálek *et al.*, 2012). Piálek *et al.* (2012) described the diversity of *Crenicichla* in the two neighboring river basins as a case of parallel evolution of two separate non-sister group clades of *Crenicichla*. They have also based on a molecular dataset utilizing predominantly mitochondrial markers (see the insufficient resolution of the only nuclear marker S7-i1 evaluated in Piálek *et al.* 2012: Figure 2) postulated that the Iguazú *Crenicichla* fauna is non-monophyletic, representing two dispersals from the middle Paraná. The authors therefore defined the evolutionary lineage from lower/middle Paraná-Iguazú basin as the *C. mandelburgeri* (the most widespread species in the middle Paraná) species complex.

Varella (2011) presented the only other taxonomic study which also included *Crenicichla* species from the Iguazú River. In agreement with our present work Varella classified the large-mouthed predator as *C. iguassuensis*. Varella's *C. yaha* agrees with what we have previously called *C. yaha* (Piálek *et al.*, 2010, 2012; Casciotta *et al.*, 2010, 2013) but which has to be called *C. tesay* as explained in Results. Because of the confusion with the names *C. yaha* and *C. tesay* Varella classified yet other populations as *C. tesay* (his Figures 34, 35) whose taxonomic status requires further study. The two new species described in the present study (*C. tuca* and *C. tapii*) were by Varella considered as conspecific variation within an undescribed species (*C.* sp. "IGUAÇU") although his own morphological analysis clearly showed that there are several characters that do not overlap signifying two distinct species (his Table 22, p. 171). We have convincingly demonstrated that not only the mouth morphology, but also coloration, ecology, morphometric characteristics, and DNA markers (Piálek et al., 2012) show that they are two completely distinct species.

The study of species diversity in complex groups such as the species complexes of *Crenicichla* pose a challenge to traditional taxonomy. Relying solely on scant morphological information from previously collected specimens without personal field information about their exact habitats, ecology, live coloration etc. can be misleading as shown in Casciotta *et al.* (2006, 2010, 2013), Casciotta and Almirón (2008), and Piálek *et al.* (2010, 2012) in the case of description and confusion between *C. yaha* and *C. tesay*, or in Varella (2011) in case of *C.* sp. "IGUAÇU". Delimiting the species from each other in such complex groups requires combining morphological obser-

vations with personal field data in order to correctly interpret the morphological variation. Even with this information there however are instances where intermediate specimens complicate the delimitation as also noted in Varella (2011). To our knowledge, however, the amounts of specimens with alien morphological traits are relatively low (probably under 5% in our study area) and we have recently started to investigate these phenomena.

The Iguazú *Crenicichla* species include the same four main ecomorphs found in the directly neighboring but distantly related *C. missioneira* species flock from the Uruguay River basin (Lucena and Kullander, 1992). The ancestral (*sensu* Piálek *et al.*, 2012) ecomorphs are the 'predators' with a long head and long prognathous piscivorous jaws (represented by *C. iguassuensis* in the Iguazú vs. *C. missioneira* and *C. celidochilus* in the Uruguay flock). The novel ecomorphs for *Crenicichla* include: 1) the small-mouthed isognathous picker/grazers with pointed lower pharyngeal teeth (*C. tapii* sp. n. vs. *C. hadrostigma*); 2) the small mouthed isognathous molluscivores with molariform lower pharyngeal teeth (*C. tesay* vs. *C. minuano*); and 3) the large-mouthed thick-lipped hypognathous cavity explorers/excavators (*C. tuca* sp. n. vs. *C. tendybaguassu*). Burress *et al.* (2013, 2015) have provided convincing support for the case that the Uruguay *Crenicichla* species flock is composed of highly adapted species with high phenotype-environment correlation and trait utility. Our examinations of the Iguazú *Crenicichla* species mirror these findings (see characteristics of species in the Taxonomy section).

The distinct morphological and ecological diversification of the four closely related sympatric species thus raises again the phylogenetic issue regarding their origin as a species flock. The novel NGS methods like RAD sequencing based on analyses of numerous nuclear loci could have the power to bring new light into their evolutionary relationships and test their potential monophyly.

MATERIAL EXAMINED

A list of comparative material of *C. scottii* and *C. vittata* is available in Casciotta (1987). In addition, the following material was studied: *Crenicichla hadrostigma* AI 220, 1, 72.8 mm SL, Argentina, Misiones, Uruguay River basin, Itacaruare. *Crenicichla hu* MACN-ict 9429, holotype, 118.0 mm SL, Argentina, Misiones, Paraná River basin, arroyo Piray–Miní. MACN-ict 9430, paratypes, 17 ex., 76.9–153.0 mm, same data as holotype. AI 261, paratypes 2 ex., 96.3–110.0 mm, same data as holotype. AI 262, paratype, 1 ex. (c&s) 93.9 mm, same data as holotype. *Crenicichla iguassuensis* FMNH 54159, holotype, 137.0 mm SL, Brazil, Rio Iguaçu, Porto União da Victoria. *Crenicichla jupiaensis*: Argentina, Corrientes, Paraná River at Yahapé: AI 226, 2, 87.7-93.0 mm SL; AI 227, 1, 60.7 mm SL. *Crenicichla lepidota*: Argentina, Buenos Aires, Isla Martín García: MACN-ict 2314, 6, 59.9-104.2 mm SL. Chaco, Esteros del Palmar: MACN-ict 7275, 1, 151.6 mm SL. Corrientes, Isla Apipé Grande, Ituzaingó: FML 312, 1, 138.0 mm SL. Entre Ríos, Uruguay River, Concepción del Uruguay: MACN-ict 4091, 1, 98.4 mm SL. Formosa, Riacho de Oro: MACN-ict 3656, 2, 116.0-165.7 mm SL. Misiones, Represa Estación Experimental Cerro Azul: MACN-ict 5067, 4, 67.7-113.4 mm SL. Salta, Luna Muerta, Hickman: FML 528, 1, 111.5 mm SL. Uruguay, Departamento Colonia, Arroyo Limetas: MNHNM 2087, 1, 72.9 mm SL. *Crenicichla cf. mandelburgeri*: Argen-

tina, Misiones, Paraná River basin, Arroyo Chapa at route 6: MACN-ict 9442, 2, 102.2-208.0 mm SL. Misiones, Paraná River basin, Arroyo Cuñapirú, at route 223 near Ruiz de Montoya: MACN-ict 9440, 2, 72.6-82.3 mm SL. Misiones, Paraná River basin, Arroyo Cuñapirú (Arroyo Tucangua): MACN-ict 9441, 7, 56.0-93.0 mm SL. Misiones, Paraná River basin, Arroyo Guaruhape at route 220: MACN-ict 9439, 2, 83.7-93.0 mm SL. *Crenicichla ocellata* MSNG 33700, holotype, 257.5 mm SL, Paraguay, Puerto 14 de Mayo, Bahía Negra, Chaco Boreal. *Crenicichla semifasciata*: Argentina, Entre Ríos, Arroyo Curupí: MACN-ict 6239, 1, 176.6 mm SL. Formosa, Riacho de Oro: MACN-ict 3683, 1, 68.8 mm SL. *Crenicichla taikyra* MACN-ict 9461, holotype, 98.3 mm, Argentina, Misiones, Paraná River at Candelaria. *Crenicichla tesay* MACN-ict 9016, holotype, 115.1 mm SL, Argentina, Misiones, Iguazú River basin, Arroyo Verde. *Crenicichla yaha*: Argentina, Misiones, Paraná River basin, Arroyo Urugua-í at Isla Palacio: MACN-ict 8924, holotype, 103.7 mm SL. Misiones, Paraná River basin, Arroyo Urugua-í at provincial route 19, Parque Provincial Islas Malvinas: MTD-F 30606, paratype, 1, 105.9 mm SL. Misiones, Paraná River basin, Arroyo Urugua-í at provincial route 19, Arroyo Uruzú, Parque Provincial Islas Malvinas: AI 200, paratype, 1, 135.8 mm SL. Misiones, Paraná River basin, Arroyo Urugua-í at Isla Palacio: AI 202, paratypes, 4(1 c&s), 37.4-48.5 mm SL. *Crenicichla ypo*: Argentina, Misiones: MACN-ict 9431, holotype, 105.5 mm SL, Paraná River basin, arroyo Urugua-í, at Establecimiento "Alto Paraná". MACN-ict 9432, paratypes 3, 101.0-116.0 mm SL, arroyo Urugua-í basin, arroyo Grapia, 6 km north from Colonia Gobernador J. J. Lanusse.

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