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Research article

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Description of two new species forming a sympatric species pair of *Crenicichla* (Teleostei: Cichlidae) endemic to the Piray Guazú River in the Paraná River Basin, Misiones, Argentina and belonging to the *C. mandelburgeri* species complex

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Abstract. *Crenicichla* is the largest and most widely distributed genus of Neotropical cichlids. The *Crenicichla mandelburgeri* species complex from the Middle Paraná departs from the ancestral and predominant ecomorphology of the large genus and shows parallel evolution of ecomorphs both within the complex and also to the unrelated *C. missioneira* species complex from the Uruguay River. Here, we formally describe a new species pair from the *C. mandelburgeri* species complex that has evolved a parallel morphological and ecological dichotomy to another species pair and also to species in the unrelated *C. missioneira* species complex. The new species pair is endemic to a single tributary (the Piray Guazú) of the Middle Paraná River where it is sympatric and partly syntopic. Mitochondrial DNA phylogeny shows the two new species as distantly related within the *C. mandelburgeri* species complex, each with a sister species in the Iguazú rather than in the neighbouring Paraná River tributaries. Nuclear DNA analyses demonstrate their sister-group relationship, which is however complicated by the reticulated origin of one of the new species. We present determination keys for all the currently formally described species of the *C. mandelburgeri* species complex including the new species described here.

Keywords. Convergence, diversification, ecomorphs, replicated evolution, species flock.

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Introduction

Crenicichla is the largest and most widely distributed genus of Neotropical cichlids (Říčan *et al*., 2021a). Within *Crenicichla* there are two species complexes which depart from the ancestral and predominant generalized predatory ecomorphology of the genus and which have formed parallel species flocks (Piálek *et al.* 2012, 2019a; Burress *et al.* 2018a, 2018b). These two complexes are found outside the Amazon in subtropical South America as part of a southern *Crenicichla* clade. The *C. mandelburgeri* species complex is one of its two parallel species complexes and is endemic to the Middle Paraná River Basin, including its main tributary, the Iguazú River (Piálek *et al.* 2012, 2019a, 2019b). The second southern species complex is the *C. missioneira* complex from the adjacent Uruguay River Basin with a parallel course to the Iguazú-Paraná River (Lucena & Kullander 1992; Piálek *et al.* 2012, 2019a; Burress *et al.* 2018a, 2018b). The *C. mandelburgeri* species complex belongs phylogenetically to the *C. lacustris* group, while the *C. missioneira* complex forms its own *C. missioneira* group, and the two complexes plus some other groups and species form the southern *Crenicichla* clade, the only clade of *Crenicichla* found mostly outside the tropics and not found in the Amazon Basin (Piálek *et al.* 2012, 2019a, 2019b; Burress *et al.* 2018a, 2018b, 2023; Říčan *et al.* 2021a, 2021b).

These two parallel *C. mandelburgeri* and *C. missioneira* species complexes are currently the best examples worldwide of parallel adaptive radiations that have occurred in rivers (Burress *et al.* 2018a). The two species complexes include apart from the ancestral generalized predatory forms (*C. gillmorlisi* Kullander & Lucena, 2013, *C. ypo* Casciotta, Almirón, Piálek, Gómez & Říčan, 2010, *C. hu* Piálek, Říčan, Casciotta & Almirón, 2010 in the *C. mandelburgeri* complex) also specialized molluscivorous species (*C. taikyra* Casciotta, Almirón, Aichino, Gómez, Piálek & Říčan, 2013, *C. tesay* Casciotta & Almirón, 2008, *C. yaha* Casciotta, Almirón & Gómez, 2006), specialized large-lipped invertebratophagous crevice feeders (*C. tuca* Piálek, Dragová, Casciotta, Almirón & Říčan, 2015), and even partially herbivorous species (periphyton grazers; *C. tapii* Piálek, Dragová, Casciotta, Almirón & Říčan, 2015), together with both benthic as well as pelagic specialized predators (invertebratophagous to piscivorous; *C. vittata* Heckel, 1840, *C. yjhui* Piálek, Casciotta, Almirón & Říčan, 2019, *C. iguassuensis* Haseman, 1911 and *C. mandelburgeri* Kullander, 2009), and all or some of these ecomorphs occur in sympatry in the Middle Paraná and the Uruguay River basins and have most probably evolved in sympatry (Piálek *et al.* 2012, 2019a, 2019b; Burress *et al.* 2018a, 2018b, 2023; Říčan *et al.* 2021a, 2021b).

The two parallel species complexes are monophyletic and highly divergent genetically, while morphologically they closely parallel each other (Piálek *et al.* 2012, 2019a; Burress *et al.* 2018a, 2018b). Morphologically the two complexes are chiefly distinguished by one colouration pattern character, i.e., a well-developed suborbital stripe in the former vs absent or greatly reduced to just a few spots in the latter, and one morphological character, i.e., the margin of the preopercular smooth vs serrated (Lucena & Kullander 1992; Piálek *et al.* 2012, 2019a, 2019b; the *C. missioneira* complex includes also *C. celidochilus* Casciotta, 1987, contrary to Lucena & Kullander 1992). The other distinguishing character is less clear-cut and includes the posttemporal blotch (unusually well developed and sometimes even ocellated vs normal) (Lucena & Kullander 1992; Casciotta *et al.* 2006; Casciotta & Almirón 2008; Kullander 2009; Casciotta *et al.* 2010, 2013; Piálek *et al.* 2010, 2015; Kullander & Lucena, 2013).

The two new species described in this study belong to the *C. mandelburgeri* species complex (Piálek *et al.* 2012, 2019a, 2019b; Burress *et al.* 2018a, 2023; Říčan *et al.* 2021a, 2012b), which currently includes 11 species. *Crenicichla vittata* Heckel, 1840 is the sister group of the complex, genetically and geographically rather distant from the species of the complex, being found outside the Middle Paraná where all other species of the complex are found (Piálek *et al.* 2012, 2019a, 2019b; Burress *et al.* 2018a, 2023; Říčan *et al.* 2021b). The whole *C. lacustris* group currently includes 30 described species (Říčan *et al.* 2021a). The 11 species of the complex in chronological order of first description are as follows:

C. iguassuensis Haseman, 1911; *C. yaha* Casciotta, Almirón & Gómez, 2006; *C. tesay* Casciotta & Almirón, 2008; *C. mandelburgeri* Kullander, 2009; *C. ypo* Casciotta *et al.* 2010; *C. hu* Piálek, Říčan, Casciotta & Almirón, 2010; *C. taikyra* Casciotta, Almirón, Aichino, Gómez, Piálek & Říčan, 2013; *C. gillmorlisi* Kullander & Lucena, 2013; *C. tapii* Piálek, Dragová, Casciotta, Almirón & Říčan, 2015; *C. tuca* Piálek, Dragová, Casciotta, Almirón & Říčan, 2015; and *C. yjhui* Piálek, Casciotta, Almirón & Říčan, 2019. It is notable that up until 2006 only one species was described from this currently large and diverse complex.

The *C. mandelburgeri* species complex is one of four clades in the *C. lacustris* species group. These four clades were convincingly recovered solely in DNA phylogenies, both mtDNA (Piálek *et al*. 2012; Říčan *et al.* 2021a) as well as nDNA (Burress *et al.* 2018a). Based on the molecular phylogenies the composition, relationships and biogeography within the *C. lacustris* group are thus as follows. The *C. mandelburgeri* complex is found in the Middle Paraná Basin including its largest affluent, the Iguazú. Its sister group is *C. vittata* from the Paraguay, Lower Paraná and Lower Uruguay, followed by the *C. jaguarensis* complex from the Upper Paraná (as first suggested by Kullander 1981, 1982; *C. jaguarensis* Haseman, 1911, *C. jupiaensis* Britski & Luengo, 1968, and probably also *Crenicichla haroldoi* Luengo & Britski, 1974, that was however never included in any phylogenetic study). The sister clade of these two Paraná lineages is a clade composed of the *C. scottii* complex from the Uruguay Basin and reaching out into the Argentinean pampas in *C. scottii* (*C. scottii* (Eigenmann, 1907), *C. gaucho* Lucena & Kullander, 1992 and *C. prenda* Lucena & Kullander, 1992) and of the *C. punctata* complex from the southern Brazilian coast (*C. punctata* Hensel, 1870, *C. maculata* Kullander & Lucena, 2006 and *C. lucenai* Mattos, Schindler, Ottoni & Cheffe, 2014). The basal clade in the *C. lacustris* group is the *C. lacustris* complex from the northern Brazilian coast (*C. lacustris* (Castelnau, 1855), *C. dorsocellata* Haseman, 1911, *C. biocellata* von Ihering, 1914, *C. iguapina* Kullander & Lucena, 2006, and *C. tingui* Kullander & Lucena, 2006; Kullander & Lucena 2006 include also *C. mucuryna* von Ihering, 1914 which was however not included in any phylogenetic analyses).

Species in the *C. lacustris* group, nor species in *Crenicichla* itself have ever been studied in a morphological phylogeny. A morphological phylogeny (that would be reconciled with the molecular phylogenies; e.g., Říčan *et al*. 2016) is needed to provide diagnoses for its species groups and complexes based on character mapping onto the phylogeny. The species groups within *Crenicichla* including the *C. lacustris* species group were thus diagnosed based on only a general characterization (Kullander 1981, 1982; Ploeg 1991; Kullander & Lucena 2006, 2013).

The *C. lacustris* group can based on this general characterization (as modified from Kullander 1982 and Kullander & Lucena 2006, 2013, with addition of subsequently discovered species) be diagnosed from the *C. missioneira* group by serrated vs smooth preopercular margin, and by suborbital stripe normally developed (except *C. jupiaensis* where as the latter) vs absent or reduced to few dots; from species of the *C. lugubris* group (including the *C. acutirostris* group) by low number of E1 scales (42–70, except *C. vitatta* with 78–85 vs 90 or more); from *C. macrophthalma* Heckel, 1840 by cycloid vs ctenoid cheek and predorsal scales, and normal size eyes vs extremely large; 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 or ocellus (from *C. hemera* Kullander, 1990 and *C. chicha* Varella, Kullander & Lima, 2012) by infraorbitals 3 and 4 separate vs co-ossified); from the *C. reticulata* group by movable vs rigidly implanted outer teeth (except the *C. scottii* complex; see below), and nostril well separated from upper lip vs close to upper lip (except in *C. cyanonotus* Cope, 1871 in which nostril distinctly separated; Kullander 1986).

Within the *C. lacustris* group the *C. mandelburgeri* species complex (sensu Piálek *et al*. 2012, 2015, 2019a, 2019b) can based on general characterization be diagnosed from the *C. lacustris* complex and

the *C. punctata* complex by usually 45–60 E1 scales (with the exception of nontype specimens of *C. iguassuensis* with 58–70 E1 scales, types with 53–59) vs usually 60–70 (range 56–75); from *C. vittata* also by less E1 scales (42–70 vs 78–85); from the *C. scottii* complex (with an overlapping number of E1 scales) by movable vs rigidly implanted outer teeth, and by tip of maxilla extending beyond anterior margin of orbit vs not or just reaching anterior margin; and among species in the *C. jaguarensis* complex (also with an overlapping number of E1 scales) from *C. haroldoi* by absence of conspicuous black spots on scales of upper lateral line vs presence, from *C. jupiaensis* and *C. jaguarensis* by absence of dominant vertical double bars that reach onto the belly (*C. jupiaensis*) or at least below midlateral line (*C. jaguarensis*) vs if present then well developed only above the midlateral line, and from *C. jupiaensis* additionally by presence of cheek scales and of suborbital stripe vs absence of both. This diagnosis of the *C. mandelburgeri* species complex also considers the two new species described in this study.

Within the *C. mandelburgeri* species complex the species diversity is structured by sub-basins of the Middle Paraná River, with the Iguazú River having the highest diversity of endemic sympatric and syntopic species (four; Piálek *et al.* 2015, plus one allopatric species, *C*. sp. Jordao; Říčan *et al.* 2017, 2021a, 2021b), followed by the Urugua-í Basin with three sympatric and partially syntopic species (*C. ypo*, *C. yaha* and *C. yjhui*; Piálek *et al.* 2012, 2019a, 2019b; Říčan *et al.* 2017, 2021a, 2021b).

The Piray Guazú Basin is the only remaining tributary of the Paraná from which more than one endemic species of *Crenicichla* are known, in this case two (Piálek *et al.* 2012, 2019a, 2019b; Říčan *et al.* 2021a, 2021b), and their formal description is the topic of this paper.

Material and methods

The Unified Species Concept was employed in the present study (de Queiroz 2007) in which species are defined as independently evolving metapopulation lineages. Our operational species-delimitation criteria were consistent morphological differences together with topology and divergence analyses in molecular phylogeny and data.

Analyses demonstrating phylogenetic relationships and molecular and morphological differentiation of the studied species have been published in previous studies, particularly in Říčan *et al.* (2021b) from which the present study directly follows, and also in Piálek *et al.* (2012, 2019a, 2019b), Burress *et al.* (2018a, 2023), and Říčan *et al.* (2021a).

Material and methods in this study are thus restricted only to those directly relevant to the taxonomic descriptions of the two new species.

Morphological methods

Voucher specimens were collected between 2007 and 2016 and are deposited in the Museo de La Plata (MLP). Specimens were cleared and counterstained (C&S) following the method of Taylor & Van Dyke (1985). Measurements and counts were taken as described by Kullander (1986) and as used and detailed in Piálek *et al.* (2010, 2015). Measurements were taken as straight line distances with digital calliper to 0.1 mm on left side of specimen. Scale row nomenclature follows Kullander (1996). Body length is expressed as standard length (SL). Morphometric characters are expressed as percents of the standard length (SL). E1 scale counts refer to the scales in the row immediately above that containing the lower lateral line (Lucena & Kullander 1992). Pharyngeal teeth description and counts of frayed zone concavities follow Casciotta & Arratia (1993). In the descriptions, the number of specimens is indicated in parentheses, and the value present in the holotype is indicated by an asterisk. Institutional abbreviations are as listed in Ferraris (2007).

Results

Taxonomy

Class Actinopterygii Klein, 1885
Order Cichliformes R. Betancur-R *et al*., 2013
Family Cichlidae Bonaparte, 1835
Genus *Crenicichla* Heckel, 1840

Crenicichla ama sp. nov.
urn:lsid:zoobank.org:act:9C8E18CF-8833-4AAA-9395-5B2D205F1997
Figs 1A, 2, 4A, 5–8; Table 1

Crenicichla sp. Piray Guazú – Piálek *et al.* 2012 (molecular phylogeny); 2019a (molecular phylogeny and genetic delimitation, photo of live specimen); 2019b (molecular phylogeny and genetic delimitation). — Říčan *et al*. 2021a (molecular phylogeny and genetic delimitation); 2021b (molecular phylogeny, genetic and morphological delimitation, photo of live specimens).

Diagnosis

Crenicichla ama sp. nov. is diagnosed from the here described sympatric *C. aravera* sp. nov. (and from *C. yjhui*, *C. vittata* and *C. mandelburgeri*) in the main colouration pattern, chiefly composed of midlateral blotches along the body side associated with variably developed vertical bars vs composed chiefly of a dominant continuous midlateral band.

Crenicichla ama sp. nov. is distinguished from all other species of the *C. mandelburgeri* species complex, i.e., those with the main body colouration chiefly composed of midlateral blotches along the body side, by having small, black spots below the midlateral blotches on occasional scales in the series 0–E3 (i.e., generally between the lower lateral line and ventral border of the midlateral blotches) vs absence of such small, black spots on the flank in *C. aravera* sp. nov., *C. hu*, *C. mandelburgeri*, *C. taikyra*, *C. yaha*, *C. yjhui*, and *C. ypo* vs similar small dark spots however all over the flank in the Iguazú species *C. iguassuensis*, *C. tesay*, *C. tuca* and males of *C. tapii* (only on posterior part of body and caudal peduncle) vs much larger dark spots and blotches all over the flank, evidently originating from the fragmentation of the flank bars in *C. gillmorlisi*. *Crenicichla ama* is further distinguished from *C. gillmorlisi* in having the dots and blotches below the midlateral blotches small and sharply defined (as in the Iguazú species) vs much larger with softer borders, and in always lacking any traces of a continuous midlateral band (vs present in most juveniles and as a trace in many adults).

Crenicichla ama sp. nov. is further distinguished from all these species (except *C. aravera* sp. nov., *C. mandelburgeri*, and *C. gillmorlisi*) by the colouration of the dorsal fin in breeding females which features a distinct dark white-margined blotch in the dorsal fin in *C. ama* (vs a long dark white-margined band in the rest).

Crenicichla ama sp. nov. is additionally distinguished from the Iguazú species *C. tapii* and *C. tuca* by having a complete series of midlateral blotches (vs only the anterior one or two blotches), and from *C. tapii*, *C. tuca*, *C. tesay*, *C. yaha* and *C. taikyra* by a different head and mouth morphology (lower jaw prognathous with normal lips vs lower jaw hypognathous with thick lips in *C. tuca*) and by much less robust LPJ and LPJ teeth. *Crenicichla ama* is distinguished from the Iguazú species *C. iguassuensis* and *C. tesay*, and from *C. gillmorlisi*, all with the same complete series of midlateral blotches, by having the spots on body usually limited only to around the ventral borders of the midlateral blotches (vs found throughout the body including the dorsum and belly in same intensity; also in *C. tuca*).

Crenicichla ama sp. nov. is most similar to *C. ypo* and *C. hu* who share the same main colouration pattern and the generalistic predatory ecomorphology (intermediate in oral jaw, LPJ jaws and teeth, and head and body proportions between all five ecomorphs of *Crenicichla*) vs *C. aravera* sp. nov., *C. yjhui*, *C. iguassuensis* and *C. mandelburgeri* which are specialized piscivorous species. *Crenicichla ama* is thus readily distinguished from *C. aravera* in lower jaw length (mean 15.7%, SD 0.63 vs 16.8% of SL, SD 0.71), upper jaw length (mean 11.7%, SD 0.38 vs 12.8% of SL, SD 0.86), head depth (mean 16.9%, SD 0.70 in *C. ama* vs 15.8% of SL, SD 1.39), more robust LPJ and LPJ teeth, body depth (mean 23.1%, SD 1.10 vs 19.8% of SL, SD 1.09, caudal peduncle depth (mean 12.8% of SL, SD 0.37 vs 11.8% of SL, SD 0.38), and pectoral fin length (mean 22.9% of SL, SD 0.87 vs 20.6% of SL, SD 0.86).

In morphometric characters *Crenicichla ama* sp. nov. is distinguished from the two most similar species *C. ypo* and *C. hu* by tendency towards longer lower jaw (*C. ama* 15.7% in SL, SD 0.63 vs *C. ypo* 14.5%, SD 2.0, vs *C. hu* 14.3%, SD 4.55), longer pectoral fin (*C. ama* 22.8% in SL, SD 1.03 vs *C. ypo* 20.1%, SD 0.84, vs *C. hu* 19.5%, SD 5.84), and larger orbit (*C. ama* 7.7% in SL, SD 0.47 vs *C. ypo* 6.4%, SD 0.37 vs *C. hu* 6.4%, SD 1.93).

Etymology

The specific epithet '*ama*' is a Guaraní word for 'rain' and is used as a noun in apposition. The name is given in allusion to the small diagnostic spots below midlateral blotches which appear as if rain (spots) is falling from clouds (midlateral blotches).

Type material

Holotype

ARGENTINA • ♂, 105.8 mm; Misiones Province, Paraná River Basin, arroyo Piray Guazú Basin, upper arroyo Piray Guazú on RP20; 26°26′34.1″ S, 54°08′29.4″ W; 18 Feb. 2012; Casciotta *et al.* leg.; MLP 11446 (Fig. 1A).

Paratypes

All from Argentina, Misiones Province, Paraná River Basin, arroyo Piray Guazú Basin.

ARGENTINA – **Misiones** • 16 ex., 83.6–111.2 mm; same collection data as for holotype; MLP 11182 (Fig. 2) • 11 ex., 67.3–103.9 mm; same collection data as for holotype; 30 Nov. 2007; Říčan *et al.* leg.; MLP 11180 (Fig. 2) • 2 ex., 75.6–84.0 mm; same collection data as for holotype; MLP 11447 • 8 ex., 77.5–150.8 mm; Paraná River Basin, Piray Guazú River Basin, tributary to upper arroyo Piray Guazú on RP16, 23 km from San Pedro; 26°35′45.90″ S, 54°16′59.96″ W; 26 Nov. 2016; Říčan leg.; MLP 11448 (Fig. 2).

Description

Body elongate, depth 4.0 to 4.8 times in SL (mean body depth 23.1% of SL, SD 1.10) (Figs 1A, 2). Head as deep as wide or slightly deeper (mean head depth 16.9% of SL, SD 0.70). Snout bluntly pointed in lateral view, 2.8 to 3.1 times in head length (mean snout length 11.4% of SL, SD 0.46). Lower jaw slightly prognathous. Tip of maxilla reaching anterior margin of orbit in most specimens. Lower lip folds widely interrupted medially. Nostrils dorsolateral. Posterior margin of preopercle serrated (27 ex.) or smooth (3 ex.). Scales on flank strongly ctenoid. Head scales cycloid. Predorsal scales small. Interopercle naked. Cheek scaled, 7 to 9 scales below eye embedded in skin. Scales in E1 row 46 (2), 47 (3), 48 (4), 49 (4), 50 (3), 51 (5), 52 (5*), 53 (2), 55 (2). Scales in transverse row 9/11 (2), 9/12 (4*), 9/13 (2), 10/11 (1), 10/12 (13), 10/13 (7), 10/14 (1). Two to three scale rows between lateral lines. Upper lateral line scales 21 (1), 22 (4), 23 (10*), 24 (9), 25 (4), 26 (2). Lower lateral line scales 8 (2), 9 (8), 10 (16), 11 (3*), 13 (1). Dorsal, anal, pectoral and pelvic fins naked. Dorsal fin XXI,9 (1); XXI,11 (12); XXI,12 (4); XXII, 9 (1); XXII,10 (1); XXII,11 (9*); XXII,12 (1); XXIII,11 (1). Anal fin III,8

(11); III,9 (18*); III,10 (1). Pectoral fin 15 (7), 16 (16*), 17 (6). Caudal-fin squamation not reaching the middle of fin. Soft-dorsal fin rounded or pointed, extending beyond caudal-fin base. Tip of anal fin not reaching caudal-fin base. Caudal fin rounded. Pectoral fin rounded, not reaching tip of pelvic fin. Microbranchiospines present on second through fourth gill arches. Gill rakers externally on first gill arch: 3 on epibranchial, 1 on angle, and 8 on ceratobranchial. Two to five patches of unicuspid teeth on fourth ceratobranchial. Lower pharyngeal tooth plate with unicuspid recurved and bicuspid crenulated curved teeth, those of posterior and medial row larger than remaining ones (Fig. 4). Upper pharyngeal tooth plate with unicuspid and bicuspid teeth. Frayed zone bearing one concavity with small unicuspid teeth. Premaxillary ascending process longer than dentigerous process. Premaxilla with unicuspid teeth on outer row, larger than inner ones. Five teeth rows near symphysis. Dentary with unicuspid teeth on outer row. Premaxillary and dentary outer row teeth slightly movable, inner ones fully depressible.

Colour in life

Background colour of body grey to greenish-grey, darker on dorsum, lighter on venter. Grey preorbital stripe between anterior margin of orbit and snout tip. Postorbital stripe between posterior margin of orbit and preopercle or opercle distal margin grey. Flanks with 6 to 8 irregular black blotches between the upper and lower lateral lines, with fainter double-bar extensions above the upper lateral line up to the dorsal-fin base. Distinct black sharply defined spots below the midlateral blotches are diagnostic for the species. Suborbital stripe black, very narrow and pointed, not reaching ventral margin of cheek. Dorsal, anal, and caudal fins pale grey, males with numerous small dark scattered dots on dorsal, anal, and caudal

Fig. 1. A. *Crenicichla ama* sp. nov., holotype, ♂ (MLP 11446, 105.8 mm). **B**. *Crenicichla aravera* sp. nov., holotype, ♂ (MLP 11450, 102.5 mm).

Fig. 2. *Crenicichla ama* sp. nov., live specimens. **A–B**. Male paratypes. **C–E**. Female paratypes. **A**. MLP 11448, tributary to upper arroyo Piray Guazú on RP16 23 km from San Pedro, 26°35′45.90″ S, 54°16′59.96″ W, November 26 2016. **B**. MLP 11182, 94.5 mm. **C–D**. MLP 11180. **E**. MLP 11448, tributary to upper arroyo Piray Guazú on RP16 23 km from San Pedro, 26°35′45.90″ S, 54°16′59.96″ W, November 26 2016).

Fig. 3. *Crenicichla aravera* sp. nov., live specimens. **A**. Holotype, ♂ (MLP 11450). **B**. Paratype, ♂ subadult (MLP 11451, 81.2 mm). **C–D**. Female paratypes (MLP 11451, 83.3 mm; MLP 11452, 93.7 mm), upper arroyo Piray Guazú on RP20, February 18 2012.

Table 1. Measurement of holotype and 29 paratypes of *Crenicichla ama* sp. nov. Standard length (SL) given in mm, proportions in percentages of SL. Abbreviation: SD = standard deviation.

	Holotype	Range	Mean	SD
Standard length (mm)	105.8	67.3–111.2		
Head length	32.9	31.8–34.4	33.0	0.61
Snout length	11.8	10.3–12.2	11.4	0.46
Lower jaw length	15.8	14.7–17.2	15.7	0.63
Upper jaw length	12.4	11.2–13.0	11.7	0.38
Head depth	17.0	15.4–18.8	16.9	0.70
Body depth	22.8	20.9–24.7	23.1	1.10
Orbital diameter	6.9	6.9–8.6	7.7	0.45
Interorbital width	7.5	6.0–7.9	6.9	0.51
Pectoral fin length	22.8	22.0–25.0	22.9	0.87
Caudal peduncle depth	12.3	12.1–13.9	12.8	0.37
Caudal peduncle length	14.7	13.9–16.5	15.0	0.69

fins, which are absent or rarely seen in females (Fig. 2). Dorsal fin of breeding females with a distinctive large black blotch margined with a white ring (Fig. 2). Reproductive females additionally with an orange band from pectoral-fin cleft to mid-body below the black midlateral markings. Caudal fin with a black subcircular spot, rarely bearing partial irregular pale ring, just above of midline of caudal fin.

Colour in alcohol

Similar to that of live specimens apart from lack of carotenoid pigments, most importantly concerning the orange area on flank of females. Main diagnostic characters, i.e., dark spots below midlateral blotches, and shape and configuration of suborbital stripe well visible (Fig. 1A) and as in live animals (Fig. 2).

Distribution

Crenicichla ama sp. nov. is endemic to the arroyo Piray Guazú Basin, Paraná River Basin, Misiones Province, Argentina (Fig. 5).

Habitat

Crenicichla ama sp. nov. is found throughout the Piray Guazú River Basin above the rapids separating it from the Paraná River (Fig. 5). The arroyo Piray Guazú is a moderately fast flowing river. It is a clear-water basin with a predominantly bouldery stream bed and running shallow water interspersed with pools (Figs 6–7). In the pools the bottom includes more silt accumulation and the pools bear macrophytes such as *Echinodorus uruguayensis* Arechav. and *Potamogeton pseudopolygonus* Hgstr.

Crenicichla aravera sp. nov.
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Figs 1B, 3, 4B, 5–8; Table 2

Crenicichla sp. Piray Guazú line – Piálek *et al.* 2012 (molecular phylogeny); 2019a (molecular phylogeny and genetic delimitation, photo of live specimen); 2019b (molecular phylogeny and genetic delimitation). — Říčan *et al*. 2021a (molecular phylogeny and genetic delimitation); 2021b (molecular phylogeny, genetic and morphological delimitation, photo of live specimens).

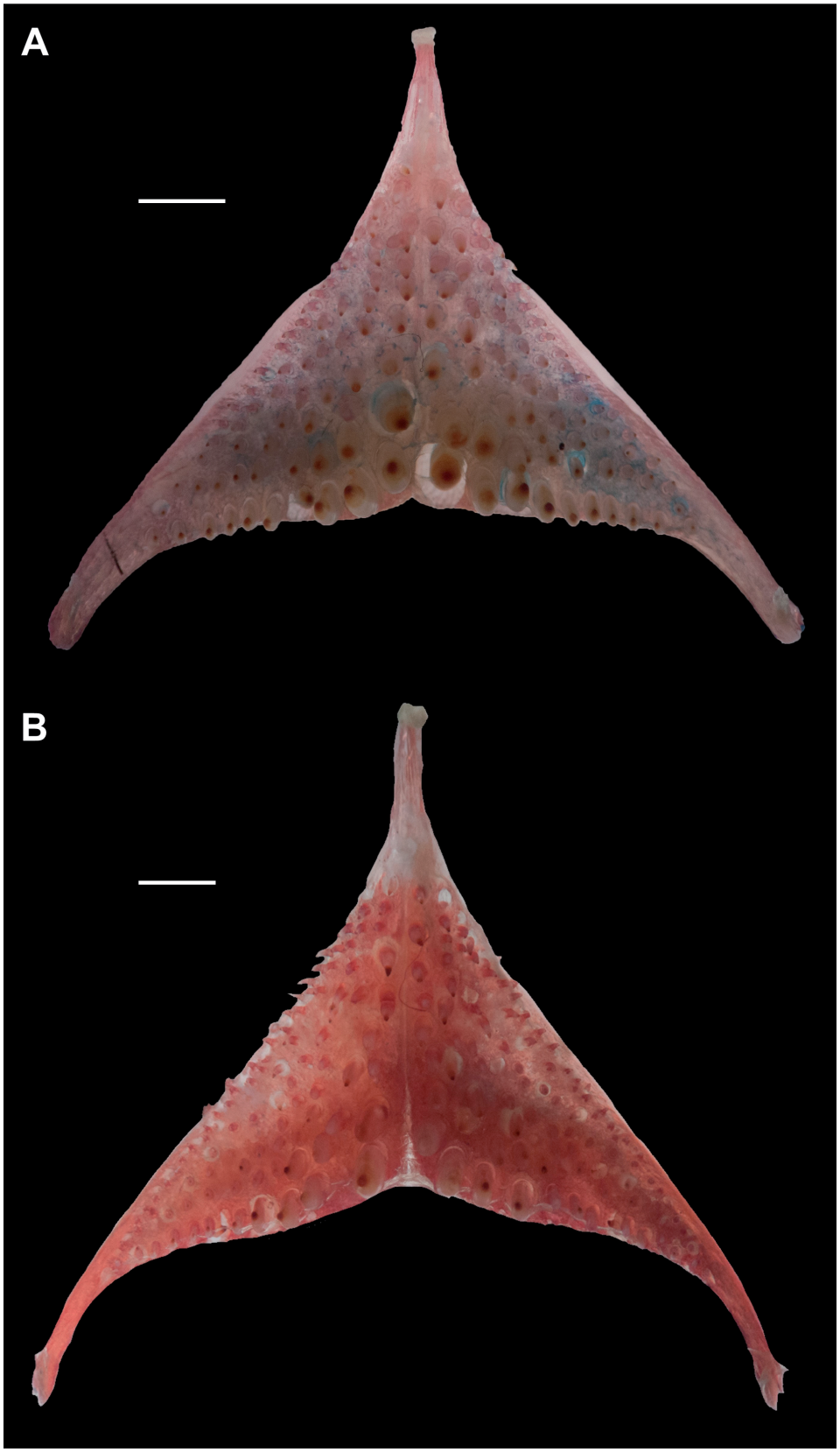

Fig. 4. Lower pharyngeal tooth plate in occlusal view. **A**. *Crenicichla ama* sp. nov., paratype (MLP 11182, 94.5 mm). **B**. *Crenicichla aravera* sp. nov., paratype (MLP 11452, 93.7 mm). Scale bars = 1 mm.

Diagnosis

Crenicichla aravera sp. nov. is diagnosed by a rare main colouration pattern (shared only with *C. yjhui* and to some extent with *C. mandelburgeri* within the *C. mandelburgeri* species complex, plus with *C. vittata*) which features a dominant continuous midlateral band vs the most common main colouration pattern composed of midlateral blotches along the body, present in all other species of the complex including *C. ama* sp. nov.

Crenicichla aravera sp. nov. is readily distinguished from *C. vittata* by 50–55 scales in E1 row (vs 78–85) and also by colouration, where the midlateral band in *C. vittata* (and in *C. mandelburgeri*) is not always present, e.g., in breeding or stressed individuals (vs always present and the dominant colouration pattern in *C. aravera*).

Crenicichla aravera sp. nov. can also be distinguished from the most similar *C. yjhui* in having less scales in E1 row (50–55 vs 53–64) and in transverse row (9/12–12/10 vs 10/13–11/16). *Crenicichla aravera* is further distinguished from *C. yjhui* in one colouration-pattern character in adult breeding females, which have a distinct dark white-margined blotch in the dorsal fin (shared with *C. ama* sp. nov. vs a long dark white-margined band in *C. yjhui*). *Crenicichla aravera* can further be marginally distinguished from *C. yjhui* in the better degree of development of all of the piscivory-associated characters, i.e., in statistically longer snout (12.1% of SL, SD 1.04 vs 11.4%, SD 0.43), longer head (33.1%, SD 0.90 vs 31.9%, SD 0.78), longer lower (16.8%, SD 0.71 vs 15.9%, SD 0.50) and upper jaws (12.8%, SD 0.86 vs 12.5%, SD 0.61), longer caudal peduncle (15.4%, SD 0.69 vs 13.6%, SD 0.76), and also in several other characters, i.e., in statistically deeper head (15.8%, SD 1.39 vs 15.1%, SD 0.64), longer pectoral fin (20.6%, SD 0.85 vs 19.5%, SD 0.98), larger eye (7.2%, SD 0.49 vs 6.8%, SD 0.47).

Crenicichla aravera sp. nov. is further diagnosed by its specialized piscivorous ecomorphology characterized by long oral jaws (mean lower jaw length 16.8% of SL, SD 0.71; mean upper jaw length 12.8% of SL, SD 0.86), shallow head (mean head depth 15.8% of SL, SD 1.39), delicate LPJs and LPJ teeth, streamlined bodies (mean body depth 19.8% of SL, SD 1.09) which it shares with *C. yjhui*, *C. iguassuensis*, *C. mandelburgeri* and with *C. tuca* (in oral jaws and head length) within the *C. mandelburgeri* species complex plus with *C. vittata* vs species with other ecomorphologies (*C. ama* sp. nov., *C. gillmorlisi*, *C. ypo*, *C. hu*, *C. taikyra*, *C. tesay*, *C. yaha*, *C. tapii* and *C. tuca* [in head depth and body depth]) with shorter oral jaws (mean lower jaw length 11.0–15.7% of SL; mean upper jaw length 9.1–11.7% of SL), deeper heads (mean head depth 16.0–18.2% of SL), more robust LPJs and LPJ teeth, and less streamlined and deeper bodies (mean body depth 22.0–24.9% of SL). *Crenicichla aravera* is further diagnosed from *C. ama* by caudal peduncle shape (mean depth 11.8% of SL, SD 0.38 vs 12.8% of SL, SD 0.37) and by pectoral fin length (mean 20.6% of SL, SD 0.86 vs 22.9% of SL, SD 0.87).

Etymology

The specific epithet '*aravera*' is a Guaraní word for 'flash' (as associated with stormy and rainy weather) and is used as a noun in apposition. The name is given in association with its sister-species *C. ama* sp. nov. (meaning rain) in allusion to the long body, pointed head, and a dominant colouration marking of a black midlateral band and rapid hunting strategy, all alluding to a flash.

Type material

Holotype

ARGENTINA • ♂, 102.5 mm; Misiones Province, Paraná River Basin, arroyo Piray Guazú Basin, upper arroyo Piray Guazú on RP20; 26°26′34.1″ S, 54°08′29.4″ W; 30 Nov. 2007; Říčan *et al.* leg.; MLP 11450 (Figs 1B, 3).

Table 2. Measurement of holotype and six paratypes of *Crenicichla aravera* sp. nov. Standard length (SL) given in mm, proportions in percentages of SL. Abbreviation: SD = standard deviation.

	Holotype	Range	Mean	SD
Standard length (mm)	102.5	81.2–135.3		
Head length	32.7	32.2–34.7	33.1	0.91
Snout length	12.2	10.6–13.7	12.1	1.04
Lower jaw length	17.6	16.2–18.1	16.8	0.72
Upper jaw length	13.2	11.5–14.4	12.9	0.87
Head depth	15.1	14.7–17.8	15.8	1.40
Body depth	19.0	18.8–21.5	19.8	1.09
Orbital diameter	7.5	6.7–7.9	7.2	0.50
Interorbital width	5.9	5.8–7.5	6.4	0.63
Pectoral fin length	20.8	19.4–21.8	20.6	0.86
Caudal peduncle depth	11.7	11.0–12.2	11.8	0.38
Caudal peduncle length	15.7	14.4–16.2	15.4	0.70

Paratypes

All from Argentina, Misiones Province, Paraná River Basin, arroyo Piray Guazú Basin, same locality as holotype.

ARGENTINA – **Misiones** • 2 ex., 81.2–83.3 mm; same collection data as for holotype; MLP 11451 (Fig. 3) • 4 ex., 2 (C&S), 90.1–135.3 mm; Paraná River Basin, arroyo Piray Guazú Basin, upper arroyo Piray Guazú on RP20; 26°26′34.1″ S, 54°08′29.4″ W; 18 Feb. 2012; Casciotta *et al.* leg.; MLP 11452 (Fig. 3).

Non-type material

ARGENTINA • 12 ex., 2 (C&S), 79.9–101 mm; Misiones Province, Paraná River Basin, arroyo Piray Guazú Basin, lower arroyo Piray Guazú at Balneario Piray Guazú; 26°29′1.66″ S, 54°35′11.98″ W; 23 Feb. 2012; Casciotta *et al.* leg.; MLP 11453.

Description

Body elongate, depth 4.6 to 5.3 times in SL (mean body depth 19.8% of SL, SD 1.09) (Figs 1B, 3). Head as deep as wide or slightly deeper (mean head depth 15.8% of SL, SD 1.39). Snout bluntly pointed in lateral view, 2.5 to 3.0 times in head length (mean snout length 12.1% of SL, SD 1.04). Lower jaw slightly prognathous. Tip of maxilla reaching anterior margin of orbit in specimens over 80.0 mm SL. Lower lip folds widely separated along symphysis. Nostrils dorsolateral. Posterior margin of preopercle serrated. Scales on flank strongly ctenoid. Head scales cycloid. Predorsal and prepelvic scales small. Interopercle naked. Cheek scaled, 8 to 11 scales below eye embedded in skin. Scales in E1 row 50 (1), 51 (1), 52 (1), 53 (1), 55 (3). Scales in transverse row 9/12 (2), 9/13 (1), 10/13 (1), 10/14 (1*), 12/10 (1). Two to three scale rows between lateral lines. Upper lateral line scales 21 (1), 23 (1), 25 (3), 26 (2*). Lower lateral line scales 8 (1), 10 (3*), 11 (2), 12 (1). Dorsal, anal, pectoral and pelvic fins naked. Dorsal fin XX,12 (1); XXI,11 (2); XXI,12 (2*); XXII,11 (1); XXIII,11 (1). Anal fin III,8 (4); III,9 (3*). Pectoral fin 16 (4); 17 (3*). Caudal-fin squamation not reaching the middle of fin. Soft-dorsal fin rounded or pointed, surpassing caudal-fin base. Tip of anal fin reaching or not caudal-fin base. Caudal fin rounded. Pectoral fin rounded, not reaching tip of pelvic fin. Microbranchiospines present on second through fourth gill arches. Gill rakers externally on first gill arch: 3 on epibranchial, 1 on angle, and 8 on

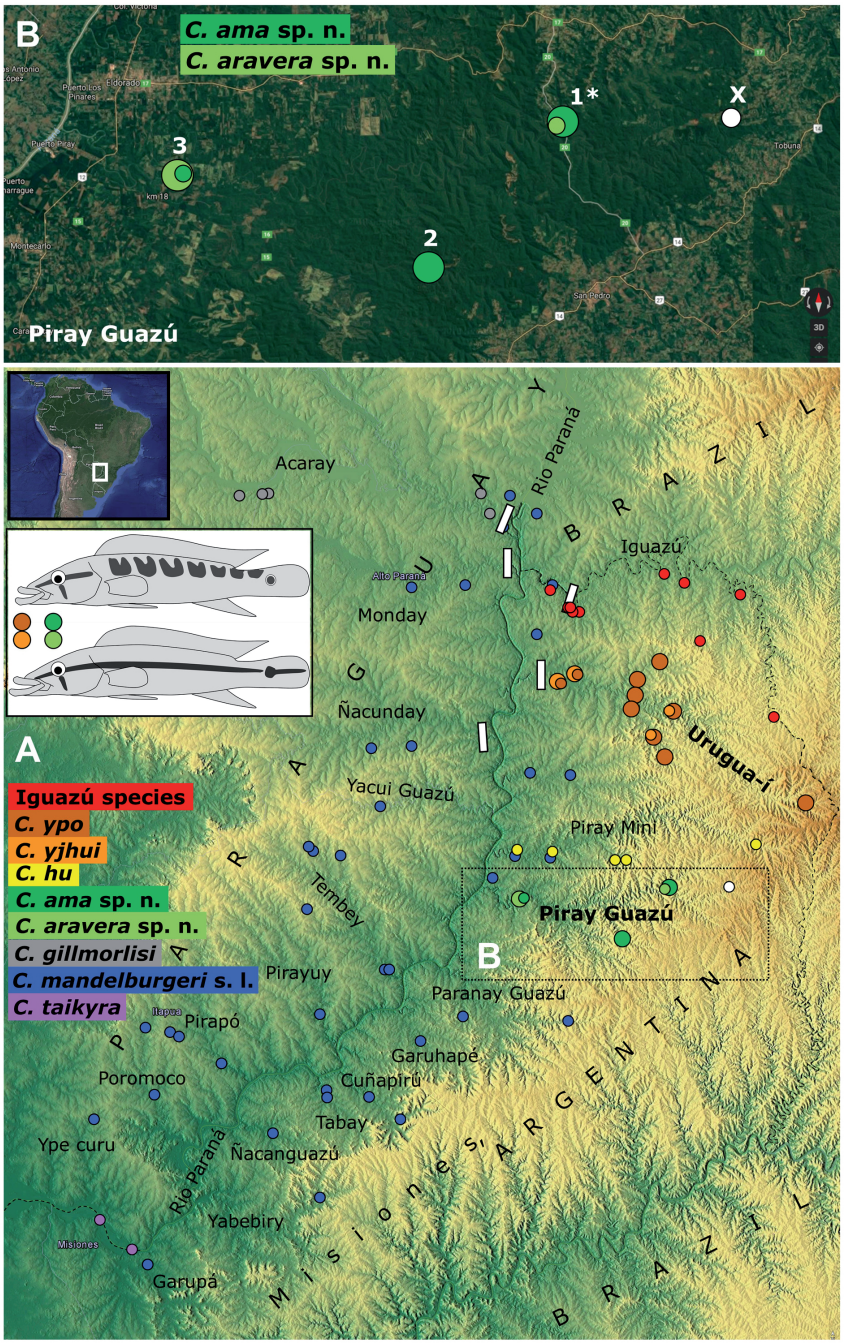

Fig. 5. A.Topographic map of the Middle Paraná Basin. **B**. Satellite map of the Piray Guazú Basin showing distribution of the sympatric *C. ama* sp. nov. (dark green) and *C. aravera* sp. nov. (light green), and also of other species in the Iguazú (red) and the Middle Paraná (*C. ypo* Casciotta, Almirón, Piálek, Gómez & Říčan, 2010: dark orange; *C. yjhui*: orange; *C. hu*: yellow; *C. mandelburgeri* sensu lato: blue, *C. gillmorlisi*: grey; *C. taikyra*: pink). Large and small dots in the Piray Guazú Basin show localities where the species is common or rare, respectively. Dark blue and light blue dots show the northern and southern mtDNA clades of *C. mandelburgeri*, respectively. White bars show location of significant waterfalls. White dot (marked with X in B) shows an upstream locality in the Piray Guazú where both *C. ama* and *C. aravera* are absent. Locality 1 (in B, marked with a star) is the type locality of both new species. Localities 2 and 3 (in B) are paratype localities of the two new species. Inset in A shows the parallel species pairs in the Piray Guazú and Urugua-í basins.

Fig. 6. Type locality of *C. ama* sp. nov. and *C. aravera* sp. nov., upper arroyo Piray Guazú on RP20 (26°26′34.1″ S, 54°08′29.4″ W), 18 February 2012.

Fig. 7. Paratype locality of *C. ama* sp. nov., tributary to upper arroyo Piray Guazú on RP16 23 km from San Pedro (26°35′45.90″ S, 54°16′59.96″ W), 26 November 2016. *Crenicichla aravera* sp. nov. is absent at this locality.

ceratobranchial. Three to five patches of unicuspid teeth on fourth ceratobranchial. Lower pharyngeal tooth plate with unicuspid recurved and bicuspid crenulated curved anteriorly teeth, those of posterior and medial row larger than remaining ones (Fig. 4). Upper pharyngeal tooth plate with unicuspid and bicuspid teeth. Frayed zone bearing one concavity with small unicuspid teeth. Premaxillary ascending process longer than dentigerous one. Premaxilla with unicuspid teeth on outer row, larger than inner ones. Five teeth rows near symphysis. Dentary with unicuspid teeth on outer row. Premaxillary and dentary outer row teeth slightly movable, inner ones fully depressible.

Colour in life

Background colour of body grey to yellowish-grey, darker on dorsum, lighter on venter, where almost white. Deep grey preorbital stripe between anterior margin of orbit and snout tip. Postorbital stripe between posterior margin of orbit and preopercle or opercle distal margin deep grey to black. Deep grey to black midlateral band along entire body as dominant colouration patter and main diagnostic character on body. Light grey hints of vertical bars only visible on dorsum above midlateral band. Suborbital stripe black, rather wide, not distinctly pointed, and short, not reaching ventral margin of cheek. Dorsal, anal, and caudal fins pale grey, males with numerous rather large dark scattered dots on dorsal, anal, and caudal fins, which are absent or rarely seen in females (Fig. 3). Dorsal fin of breeding females with distinctive large black blotch (Fig. 3). Females additionally with more yellow tones below midlateral band, in reproductive females likely more intensified into an orange band from pectoral-fin cleft to mid-body. Caudal fin with a black subcircular spot, rarely bearing a partial irregular pale ring, just above of midline of caudal fin.

Colour in alcohol

Similar to that of live specimens apart from lack of carotenoid pigments, most importantly of orange area on flank of females. Main diagnostic characters, i.e., black continuous midlateral band with spot-shaped irregularities on ventral margin, and shape and configuration of suborbital stripe well preserved (Fig. 1B) and as in live animals (Fig. 3).

Distribution

Crenicichla aravera sp. nov. is endemic to the arroyo Piray Guazú Basin, Paraná River Basin, in Misiones Province, Argentina (Fig. 5).

Habitat

Crenicichla aravera sp. nov. is only found in the Piray Guazú Basin above the rapids separating it from the Paraná River, but has so far only been collected from the main river channel (Fig. 5), unlike *C. ama* sp. nov., which is also known from tributaries. *Crenicichla aravera* is syntopic with *C. ama*. Other details concerning the arroyo Piray Gauzú as given for *C. ama*.

Keys to the species of Crenicichla from the Middle Rio Paraná Basin (the Crenicichla mandelburgeri species group plus C. vittata)

Because of the taxonomical and morphological complexity of the *C. mandelburgeri* species complex we have chosen to provide two determination keys, each primarily based on a different main character. We believe this may facilitate determination of some species.

The first key is more suited to the present study as it is based on the main colouration patterns, which also distinguish the two newly described species.

The second key is more generally suited to the *C. mandelburgeri* species complex and the existing literature on parallel evolution of ecomorphologies in *Crenicichla* since it is based on oral jaw characteristics (the main charaters involved in the formation and parallel evolution of ecomorphs).

For the keys we have chosen to use only readily visible external characters. Many of the characters used in the key will work only for adult specimens (at least 70 mm SL), especially the colour and colouration pattern characters. The main colouration pattern of the species is scored based on preserved specimens where there is less variation than in live specimens, while the colouration of the dorsal fin in females is best visible in live specimens.

Key to the species of *Crenicichla* from the Middle Rio Paraná Basin (the *Crenicichla mandelburgeri* species group plus *C. vittata*) based on the main colouration pattern

1. Main colouration pattern of adults chiefly or most often composed of a dominant continuous midlateral band, in the latter case sometimes in combination with vertical bars 2
– Main colouration pattern of adults chiefly composed of midlateral blotches along the body side without any continuous midlateral band 5
– Main colouration pattern chiefly composed of paired vertical bars in young, and fragmented into dark blotches and spots all over the sides including side of belly in adults, midlateral band when present is continuous, endemic to the Acaray tributary, endemic to Paraguay .... ***C. gillmorlisi*** Kullander & Lucena, 2013

2. The midlateral band is always present as a dominant colouration pattern in all growth stages, moods and under other conditions, scales in E1 row 50–64 3
– Depending on growth stage, mood and other factors the dominant body colouration can change from a midlateral band to vertical bars, or be a combination of the two, scales in E1 row either 42–57 or 78–85 4

3. Breeding females with a distinct dark white-margined blotch in the dorsal fin, scales in E1 row 50–55, endemic to the Piray Guazú tributary, endemic to Argentina ..... ***C. aravera*** sp. nov.
– Breeding females with a distinct dark white-margined long band in the dorsal fin, scales in E1 row 53–64, endemic to the Urugua-í tributary, endemic to Argentina .... ***C. yjhui*** Piálek, Casciotta, Almirón & Říčan, 2019

4. Midlateral band when present always fully continuous, with barely discernible fluctuation in width, scales in E1 row 78–85, widespread in the Lower Paraná and entire Paraguay Basin, also present in Lower Uruguay and lower portions of the Middle Paraná in Paraguay, Brazil, Argentina and Uruguay ..... ***C. vittata*** Heckel, 1840
– Midlateral band often semicontinuous or even distrupted (i.e., always of clearly fluctuating width), vertical bars when present always as clear double-bars, scales in E1 row 42–57, endemic to Middle Paraná main River and some non-isolated tributaries in Paraguay and Argentina .... ***C. mandelburgeri*** Kullander, 2009

5. Breeding females with a distinct dark white-margined blotch in the dorsal fin, scattered spots on body below the midlateral band in both sexes, especially in males, endemic to the Piray Guazú tributary, endemic to Argentina ..... ***C. ama*** sp. nov.
– Breeding females with a distinct dark white-margined long band in the dorsal fin 6

6. Scattered spots on body below the midlateral band in both sexes, especially in males, endemic to the Iguazú, Argentina and Brazil 7
– Without spots on body below the midlateral band in both sexes, endemic to Middle Paraná Basin apart from the Iguazú 10

7. Oral jaws prognathous (i.e., lower jaw projecting in front of upper jaw), mouth large, corner of mouth reaching well below eye ..... ***C. iguassuensis*** Haseman, 1911
– Oral jaws isognathous or hypognathous (i.e., upper jaw projecting in front of lower jaw) 8

8. Mouth large, corner of mouth reaching below vertical from anterior margin of eye, lips very thick and bulbous ..... ***C. tuca*** Piálek, Dragová, Casciotta, Almirón & Říčan, 2015
– Mouth small, not reaching eye, lips normal 9

9. Well-developed vertical double-bars (only species in the Iguazú with this character), anterior one or two midlateral blotches much more dominant over the remaining, which are usually only visible as connections between the double bars, a well-formed (not decomposed into spots) narrow suborbital stripe inclined significantly posteriad, near absence of dark scattered dots on flanks in males and complete absence in females ..... ***C. tapii*** Piálek, Dragová, Casciotta, Almirón & Říčan, 2015
– Vertical bars and less developed double bars only visible above midlateral line, anterior four or more midlateral blotches well dominant, suborbital stripe decomposed into spots, wider, and less inclined posteriad, both sexes with dark scattered dots on flanks ..... ***C. tesay*** Casciotta & Almirón, 2008

10. Oral jaws prognathous (i.e., lower jaw projecting in front of upper jaw), mouth rather large (i.e., corner of mouth reaching below vertical from anterior margin of eye) 11
– Oral jaws isognathous or hypognathous (i.e., upper jaw projecting in front of lower jaw), mouth rather small (i.e., not reaching eyes) 12

11. Anterior two to three midlateral blotches dominant, background colouration light grey, midlateral blotches distinctly H-like with dorsally continuing double bars, females with a wide wide orange to red stripe along the entire length of the basal portion of the dorsal fin above which is found a shorter black band margined in white, suborbital stripe of normal length and width, composed of spots, which do not form horizontal lines, endemic to the Urugua-í tributary, endemic to Argentina .... ***C. ypo*** Casciotta, Almirón, Piálek, Gómez & Říčan, 2010
– All midlateral blotches well developed, background colouration very dark grey to blackish, midlateral blotches square-like with dorsally continuing single wide bars, females only with the shorter black band margined in white in the dorsal fin without the orange to red band, suborbital stripe short and wide, ventrally widest, composed of spots which do form horizontal lines, endemic to the Piray Miní tributary, endemic to Argentina ..... ***C. hu*** Piálek, Říčan, Casciotta & Almirón, 2010

12. Anterior two to three midlateral blotches usually more dominant, midlateral blotches distinctly H-like with dorsally continuing double bars, suborbital stripe shorter and wider, composed of spots which tend to form horizontal lines, scales in E1 row 48–51 (mean 50), endemic to the Urugua-í tributary, endemic to Argentina ..... ***C. yaha*** Casciotta, Almirón & Gómez, 2006
– All midlateral blotches equally developed, midlateral blotches square-like with dorsally continuing single wide bars, suborbital stripe of normal length and width, composed of spots which tend to form horizontal lines, scales in E1 row 54–60 (mean 56–57), endemic to the lower portion of the Middle Paraná and some non-isolated tributaries in Paraguay and Argentina .... ***C. taikyra*** Casciotta, Almirón, Aichino, Gómez, Piálek & Říčan, 2013

Key to the species of *Crenicichla* from the Middle Rio Paraná Basin (the *Crenicichla mandelburgeri* species group plus *C. vittata*) based on oral jaw characteristics

1. Oral jaws isognathous or hypognathous (i.e., upper jaw projecting in front of lower jaw), mouth generally rather small to small (i.e., not reaching eyes), except in one species where quite large ... 2
– Oral jaws prognathous (i.e., lower jaw projecting in front of upper jaw), mouth rather large to large (i.e., corner of mouth reaching below vertical from anterior margin of eye) 6

2. Mouth large, corner of mouth reaching below vertical from anterior margin of eye, lips very thick and bulbous ..... ***C. tuca*** Piálek, Dragová, Casciotta, Almirón & Říčan, 2015
– Mouth small, not reaching eye, lips normal 3

3. Scattered spots on body below the midlateral band in both sexes, especially in males (except for one species where weakly developed), endemic to the Iguazú, Argentina and Brazil 4
– Without spots on body below the midlateral band in both sexes, endemic to Middle Paraná Basin apart from the Iguazú 5

4. Well-developed vertical double-bars (only species in the Iguazú with this character), anterior one or two midlateral blotches much more dominant over the remaining, which are usually only visible as connections between the double bars, a well-formed (not decomposed into spots) narrow suborbital stripe inclined significantly posteriad, near absence of dark scattered dots on flanks in males and complete absence in females ..... ***C. tapii*** Piálek, Dragová, Casciotta, Almirón & Říčan, 2015
– Vertical bars and less developed double bars only visible above midlateral line, anterior four or more midlateral blotches well dominant, suborbital stripe decomposed into spots, wider, and less inclined posteriad, both sexes with dark scattered dots on flanks ..... ***C. tesay*** Casciotta & Almirón, 2008

5. Anterior two to three midlateral blotches usually more dominant, midlateral blotches distinctly H-like with dorsally continuing double bars, suborbital stripe shorter and wider, composed of spots which tend to form horizontal lines, scales in E1 row 48–51 (mean 50), endemic to the Urugua-í tributary, endemic to Argentina ..... ***C. yaha*** Casciotta, Almirón & Gómez, 2006
– All midlateral blotches equally developed, midlateral blotches square-like with dorsally continuing single wide bars, suborbital stripe of normal length and width, composed of spots which tend to form horizontal lines, scales in E1 row 54–60 (mean 56–57), endemic to the lower portion of the Middle Paraná and some non-isolated tributaries in Paraguay and Argentina .... ***C. taikyra*** Casciotta, Almirón, Aichino, Gómez, Piálek & Říčan, 2013

6. Main colouration pattern of adults chiefly or most often composed of a dominant continuous midlateral band, in the latter case sometimes in combination with vertical bars 7
– Main colouration pattern of adults chiefly composed of midlateral blotches along the body side without any continuous midlateral band 11
– Main colouration pattern chiefly composed of paired vertical bars in young, and fragmented into dark blotches and spots all over the sides including side of belly in adults, midlateral band when present is continuous, endemic to the Acaray tributary, endemic to Paraguay .... ***C. gillmorlisi*** Kullander & Lucena, 2013

7. The midlateral band is always present as a dominant colouration pattern in all growth stages, moods and under other conditions, scales in E1 row 50–64 8
– Depending on growth stage, mood and other factors the dominant body colouration can change from a midlateral band to vertical bars, or be a combination of the two, scales in E1 row either 42–57 or 78–85 9

8. Breeding females with a distinct dark white-margined blotch in the dorsal fin, scales in E1 row 50–55, endemic to the Piray Guazú tributary, endemic to Argentina ..... ***C. aravera*** sp. nov.
– Breeding females with a distinct dark white-margined long band in the dorsal fin, scales in E1 row 53–64, endemic to the Urugua-í tributary, endemic to Argentina .... ***C. yjhui*** Piálek, Casciotta, Almirón & Říčan, 2019

9. Midlateral band when present always fully continuous, with barely discernible fluctuation in width, scales in E1 row 78–85, widespread in the Lower Paraná and entire Paraguay Basin, also present in Lower Uruguay and lower portions of the Middle Paraná in Paraguay, Brazil, Argentina and Uruguay ..... ***C. vittata*** Heckel, 1840
– Midlateral band most often semicontinuous or even distrupted (i.e., always of clearly fluctuating width), vertical bars when present always as clear double-bars, scales in E1 row 42–57, endemic to Middle Paraná main River and some non-isolated tributaries in Paraguay and Argentina .... ***C. mandelburgeri*** Kullander, 2009

10. Breeding females with a distinct dark white-margined blotch in the dorsal fin, a few scattered spots on body below the midlateral band in both sexes, especially in males, endemic to the Piray Guazú tributary, endemic to Argentina ..... ***C. ama*** sp. nov.
– Breeding females with a distinct dark white-margined long band in the dorsal fin 11

11. Scattered spots on body below the midlateral band in both sexes, especially in males, endemic to the Iguazú, Argentina and Brazil ..... ***C. iguassuensis*** Haseman, 1911
– Without spots on body below the midlateral band in both sexes, endemic to Middle Paraná Basin apart from the Iguazú, endemic to Argentina 12

12. Anterior two to three midlateral blotches dominant, background colouration light grey, midlateral blotches distinctly H-like with dorsally continuing double bars, females with a wide wide orange to red stripe along the entire length of the basal portion of the dorsal fin above which is found a shorter black band margined in white, suborbital stripe of normal length and width, composed of spots, which do not form horizontal lines, endemic to the Urugua-í tributary, endemic to Argentina ....***C. ypo*** Casciotta, Almirón, Piálek, Gómez & Říčan, 2010
– All midlateral blotches well developed, background colouration very dark grey to blackish, midlateral blotches square-like with dorsally continuing single wide bars, females only with the shorter black band margined in white in the dorsal fin without the orange to red band, suborbital stripe short and wide, ventrally widest, composed of spots which do form horizontal lines, endemic to the Piray Miní tributary, endemic to Argentina .....***C. hu*** Piálek, Říčan, Casciotta & Almirón, 2010

Discussion

Crenicichla ama sp. nov. and *C. aravera* sp. nov. are sympatric species endemic to the arroyo Piray Guazú Basin, Paraná River Basin, in Misiones Province, Argentina (Fig. 5).

Crenicichla ama sp. nov. and *C. aravera* sp. nov. feature highly different main colouration patterns within the *C. mandelburgeri* species complex (see Piálek *et al.* 2019a for photos of all species). *Crenicichla ama* features the most common main colouration pattern within the *C. mandelburgeri* species complex, which is chiefly composed of midlateral blotches along the body side associated with variably developed vertical bars (see Piálek *et al.* 2019a for photos of all species), and which is also present in the following species: *C. gillmorlisi*, *C. hu*, *C. iguassuensis*, *C. taikyra*, *C. tapii*, *C. tesay*, *C. tuca*, *C. yaha*, and *C. ypo.*

Crenicichla aravera sp. nov. on the other hand features a rare main colouration pattern within the *C. mandelburgeri* species complex, which it shares solely with *C. yjhui* and to some degree with *C. vittata* and *C. mandelburgeri* (see Diagnosis and Keys). This rare main colouration pattern features a dominant continuous midlateral band; see Piálek *et al.* 2019a for photos of all species).

In breeding colouration *Crenicichla aravera* sp. nov. adult females generally display a less distinctly developed orange band along the flank compared to *C. ama* sp. nov., but the extent and intensity of this band varies both intra- and inter-specifically and the band is present in breeding females of all species of the *C. mandelburgeri* complex including *C. vittata*.

Morphometric data as analysed through multivariate principal component analyses (Fig. 8D; Říčan *et al.* 2021b: figs 8–9) show complete separation of the sympatric *C. ama* sp. nov. and *C. aravera* sp. nov. In morphometric characters *Crenicichla aravera* is distinguished from *C. ama* by longer jaws while all other measurements (except snout length) have larger proportional values in *C. ama* (see Diagnosis). Among these body depth, head depth, caudal peduncle depth, and pectoral fin length are the most significant with little or no overlap (Tables 1–3).

Table 3. Proportional measurements in percentages of standard length of *C. ama* sp. nov., *C. aravera*, *C. yjhui*, and *C. ypo* Casciotta, Almirón, Piálek, Gómez & Říčan, 2010. Abbreviation: SD = standard deviation.

	***C. ama* (N = 30)**			***C. aravera* (N = 7)**			***C. yjhui* (N = 25)**			***C. ypo* (N = 17)**		
	Range	**Mean**	**SD**	**Range**	**Mean**	**SD**	**Range**	**Mean**	**SD**	**Range**	**Mean**	**SD**
Standard length (mm)	67.3–111.2			81.2–135.3			83.5–142.2			89.8–137.0		
Head length	31.8–34.4	33.0	0.61	32.2–34.7	33.1	0.91	29.7–33.3	31.9	0.78	32.0–34.6	33.2	0.76
Snout length	10.3–12.2	11.4	0.46	10.6–13.7	12.1	1.04	10.6–12.3	11.5	0.43	10.8–12.8	11.8	0.64
Lower jaw length	14.7–17.2	15.7	0.63	16.2–18.1	16.8	0.72	15.3–17.1	16.0	0.50	13.7–16.2	14,6	0.63
Upper jaw length	11.2–13.0	11.7	0.38	11.5–14.4	12.9	0.87	11.4–13.7	12.5	0.62	11.1–12.9	11.6	0.38
Head depth	15.4–18.8	16.9	0.70	14.7–17.8	15.8	1.40	13.4–16.2	15.1	0.65	14.5–17.6	16.0	0.97
Body depth	20.9–24.7	23.1	1.10	18.8–21.5	19.8	1.09	18.3–21.9	20.0	1.12	20.5–23.9	22.3	1.05
Orbital diameter	6.9–8.6	7.7	0.45	6.7–7.9	7.2	0.50	6.2–7.7	6.8	0.48	5.7–7.1	6.4	0.37
Interorbital width	6.0–7.9	6.9	0.51	5.8–7.5	6.4	0.63	5.2–7.0	6.1	0.43	6.2–7.9	7.1	0.50
Pectoral fin length	22.0–25.0	22.9	0.87	19.4–21.8	20.6	0.86	17.2–21.1	19.5	0.99	18.7–22.0	20.1	0.84
Caudal peduncle depth	12.1–13.9	12.8	0.37	11.0–12.2	11.8	0.38	10.2–11.6	10.8	0.40	10.9–12.9	12.1	0.60
Caudal peduncle length	13.9–16.5	15.0	0.69	14.4–16.2	15.4	0.70	12.3–14.8	13.6	0.76	14.3–16.7	15.5	0.55

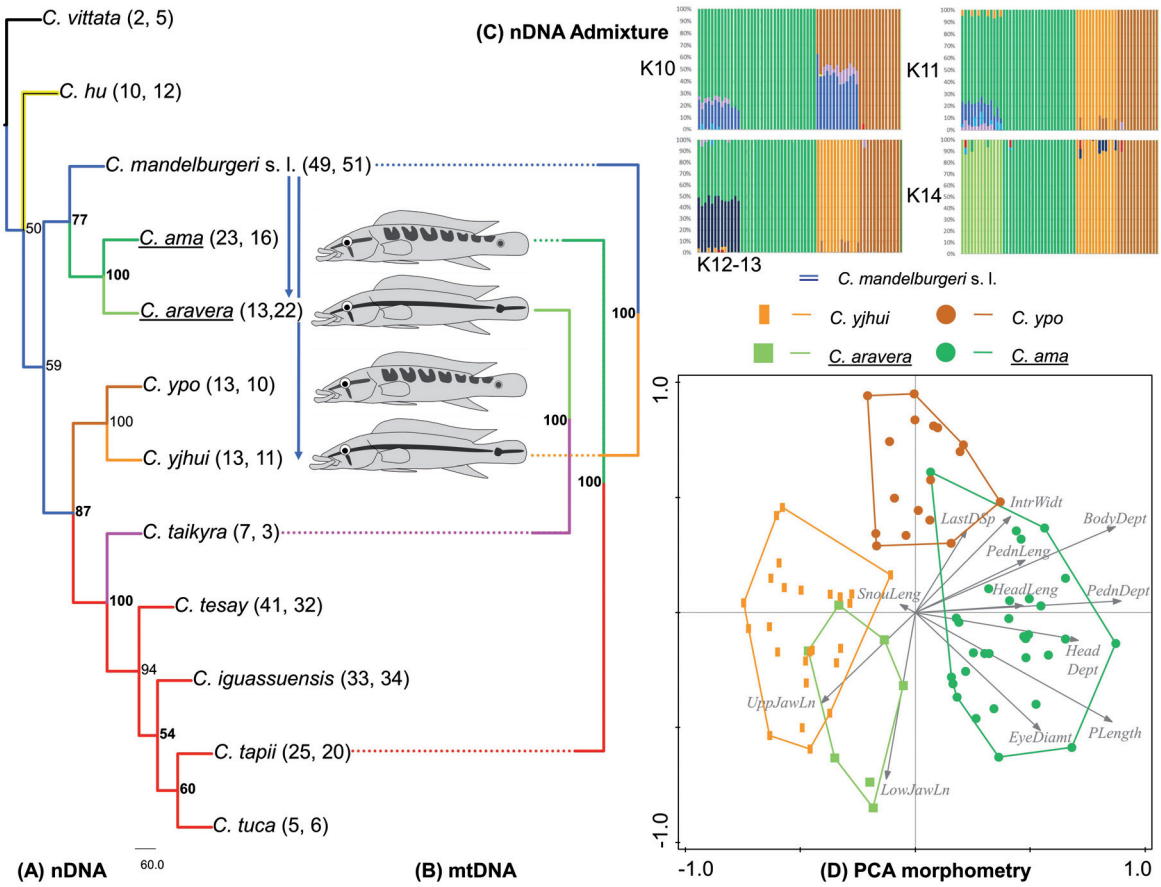

Fig. 8. Overview of phylogenetic relationships and molecular and morphological differentiation of *C. ama* sp. nov. and *C. aravera* sp. nov. and its parallel species pair (*C. ypo* Casciotta, Almirón, Piálek, Gómez & Říčan, 2010 and *C. yjhui* Piálek, Casciotta, Almirón & Říčan, 2019). **A**. Summary of phylogenetic relationships within the *C. mandelburgeri* species complex with a nDNA ddRAD SVDQ species tree analysis as main topology focusing on the parallel species pairs in the Piray Guazú (the two new species) and Urugua-í River basins. Species tree is based on 60% SNP-representation matrix using fixed (= homozygotic sites). Red and blue basal branches and nodes in the species tree topology show biogeography (Red: Iguazú, Blue: Middle Paraná). Numbers in parentheses are total numbers of analyzed individuals (in nDNA/in mtDNA). Numbers at nodes show bootstrap support values. Species colours as in Fig. 5. Blue arrows show nDNA introgression from *C. mandelburgeri* into *C. aravera* and *C. yjhui*. Modified from Říčan *et al.* (2021b). **B**. Alternative topology to the right of the tree represents mtDNA relationships of species in the two focal species pairs. Only *C. ypo* does not have a mitonuclear phylogenetic conflict. Modified from Říčan *et al.* (2021b). **C**. Inference of population structure based on the Admixture analysis for the two focal species pairs. Note majority assignment of *C. yjhui* and *C. aravera* with *C. ypo* and *C. ama* and partial assignment to *C. mandelburgeri* sensu lato at K10 to K13, and complete separation of all species at K14. Modified from Říčan *et al.* (2021b). **D**. Morphometric variation and discrimination of the two species pairs of sympatric species from the Piray Guazú (*C. ama*, *C. aravera*) and Urugua-í (*C. ypo*, *C. yjhui*) River basins analyzed by PCA based on holotype and paratype specimens ≥70 mm SL. Morphological measurements followed Kullander's (1986) methodology for *Crenicichla* Heckel, 1840 and were used as proportional values in % of SL. Note complete separation of species between ecomorphs (sympatric) and partial separation within ecomorphs (allopatric). Modified from Říčan *et al.* (2021b).

The two newly described species form a parallel morphological species pair to *C. ypo* and *C. yjhui* from the Urugua-í River (Říčan *et al.* 2021b). *Crenicichla ama* sp. nov. is best distinguished from the most similar species *C. ypo* (and from the in colouration patterns even more similar *C. hu*) by colouration patterns and by longer jaws, pectoral fin and larger orbit while the two latter species have longer snouts, caudal peduncles and interorbital widths (see Diagnosis and Říčan *et al.* 2021b: fig. S1). *Crenicichla aravera* sp. nov. is also best distinguished from the parallel species *C. yjhui* by colouration patterns and morphometric data, by longer jaws, longer snout, longer and deeper head, deeper caudal peduncle, larger eye and longer pectoral fin (see Diagnosis and Říčan *et al.* 2021b: fig. S2).

Crenicichla ama sp. nov. and *C. aravera* sp. nov. are also clearly differentiated in molecular characters, in both mitochondrial (mtDNA; ND2 and cytb) and nuclear (nDNA; ddRAD) genomes (Fig. 8A–B; Piálek *et al.* 2012, 2019a, 2019b; Říčan *et al.* 2021a, 2021b). In phylogenetic analyses of mtDNA (Piálek *et al.* 2012, 2019a, 2019b; Říčan *et al.* 2021a, 2021b) *C. ama* and *C. aravera* are not closely related and each belongs to a different clade (Fig. 8B). In phylogenetic species-tree analyses as well as population-based analyses of the nDNA data (Admixture, FineRADstructure, TreeMix analyses) *C. ama* and *C. aravera* are strongly supported as sister species (Fig. 8A, C; Piálek *et al.* 2019a, 2019b; Říčan *et al.* 2021b).

Both the phylogenetic and population admixture analyses of molecular data thus demonstrate strong genetic differentiation of *C. ama* sp. nov. and *C. aravera* sp. nov. The genetic differentiation of *C. ama* and *C. aravera* parallels the situation in the parallel species pair *C. ypo* and *C. yjhui* (Fig. 8A–C). The generalistic predatory species *C. ama* and *C. ypo* show genetic differentiation without mixed ancestry and both species show coancestry with their sympatric piscivorous species, *C. aravera* and *C. yjhui*, respectively. The piscivorous *C. aravera* and *C. yjhui* however additionally show secondary admixture from *C. mandelburgeri* s. lat. (Fig. 8C). The two species pairs (*C. ama* and *C. aravera*, *C. ypo* and *C. yjhui*) thus not only show parallel morphological evolution but also a parallel pattern of genetic differentiation.

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References

Burress E.D., Piálek L., Casciotta J.R., Almirón A., Tan M., Armbruster J.W. & Říčan O. 2018a. Island- and lake-like parallel adaptive radiations replicated in rivers. *Proceedings of the Royal Society B* 285: 20171762. https://doi.org/10.1098/rspb.2017.1762

Burress E.D., Alda F., Duarte A., Loureiro M., Armbruster J.W. & Chakrabarty P. 2018b. Phylogenomics of pike cichlids (Cichlidae: *Crenicichla*): the rapid ecological speciation of an incipient species flock. *Journal of Evolutionary Biology* 31: 14–30. https://doi.org/10.1111/jeb.13196

Burress E.D., Piálek L., Casciotta J.R., Almirón A. & Říčan O. 2023. Rapid parallel morphological and mechanical diversification of South American pike cichlids (*Crenicichla*). *Systematic Biology* 72 (1): 120–133. https://doi.org/10.1093/sysbio/syac018

Casciotta J. & Almirón A. 2008. *Crenicichla tesay*, a new species of cichlid (Perciformes: Labroidei) from the rio Iguazu basin in Argentina. *Revue suisse de Zoologie* 115: 651–659. https://doi.org/10.5962/bhl.part.80451

Casciotta J.R. & Arratia G. 1993. Jaws and teeth of American Cichlids (Pisces: Labroidei). *Journal of Morphology* 217: 1–36. https://doi.org/10.1002/jmor.1052170102

Casciotta J., Almirón A.E. & Gómez S.E. 2006. *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., Almirón A., Piálek L., Gómez S. & Říčan O. 2010. *Crenicichla ypo* (Teleostei: Cichlidae), a new species from the middle Paraná basin in Misiones, Argentina. *Neotropical Ichthyology* 8: 643–648. https://doi.org/10.1590/S1679-62252010000300009

Casciotta J., Almirón A., Aichino D., Gómez S., Piálek L. & Říčan O. 2013. *Crenicichla taikyra* (Teleostei: Cichlidae), a new species of pike cichlid from the middle río Paraná, Argentina. *Zootaxa* 3721 (4): 379–386. https://doi.org/10.11646/zootaxa.3721.4.5

de Queiroz K. 2007. Species concepts and species delimitation. *Systematic Biology* 56: 879–886. https://doi.org/10.1080/10635150701701083

Ferraris C.J. 2007. Checklist of catfishes, recent and fossil (Osteichthyes: Siluriformes), and catalogue of siluriform primary types. *Zootaxa* 1418 (1): 1–628. https://doi.org/10.11646/zootaxa.1418.1.1

Haseman J.D. 1911. An annotated catalog of the cichlid fishes collected by the expedition of the Carnegie Museum to central South America, 1907-10. *Annals of the Carnegie Museum* 7: 329–373. Available from https://www.biodiversitylibrary.org/page/9956994 [accessed 2 Jun. 2023].

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. https://doi.org/10.5962/bhl.part.82400

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. https://doi.org/10.5962/bhl.part.82465

Kullander S.O. 1986. *The Cichlid Fishes of the Amazon River Drainage of Peru*. Swedish Museum of Natural History, Stockholm.

Kullander S.O. 1996. *Heroina isonycterina*, a new genus and species of cichlid fish from Western Amazonia, with comments on cichlasomine systematics. *Ichthyological Exploration of Freshwaters* 7: 149–172.

Kullander S.O. 2009. *Crenicichla mandelburgeri*, a new species of cichlid fish (Teleostei: Cichlidae) from the Paraná river drainage in Paraguay. *Zootaxa* 2006 (1): 41–50. https://doi.org/10.11646/zootaxa.2006.1.3

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 (2): 127–146. https://doi.org/10.1590/S1679-62252006000200001

Kullander S.O. & Lucena C.A.S. 2013. *Crenicichla gillmforlisi*, a new species of cichlid fish (Teleostei: Cichlidae) from the Paraná river drainage in Paraguay. *Zootaxa* 3641 (2): 149–164. https://doi.org/10.11646/zootaxa.3641.2.3

Lucena C.A.S. & Kullander S.O. 1992. The *Crenicichla* (Teleostei: Cichlidae) 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 (1): 33–46. https://doi.org/10.11646/zootaxa.2537.1.3

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. https://doi.org/10.1016/j.ympev.2011.09.006

Piálek L., Dragová K., Casciotta J., Almirón A. & Říčan O. 2015. 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*. *Historia Natural (Tercera Serie)* 5: 5–27.

Piálek L., Burress E., Dragová K., Almirón A., Casciotta J. & Říčan O. 2019a. Phylogenomics of pike cichlids (Cichlidae: *Crenicichla*) of the *C. mandelburgeri* species complex: rapid ecological speciation in the Iguazú River and high endemism in the Middle Paraná basin. *Hydrobiologia* 832: 355–375. https://doi.org/10.1007/s10750-018-3733-6

Piálek L., Casciotta J., Almirón A. & Říčan O. 2019b. A new pelagic predatory pike cichlid (Teleostei: Cichlidae: *Crenicichla*) from the *C. mandelburgeri* species complex with parallel and reticulate evolution. *Hydrobiologia* 832: 377–395. https://doi.org/10.1007/s10750-018-3754-1

Ploeg A. 1991. *Revision of the South American Cichlid Genus Crenicichla Heckel, 1840 with Descriptions of Fifteen New Species and Considerations on Species Groups, Phylogeny and Biogeography (Pisces, Perciformes, Cichlidae)*. Akademisch Proefschrift, Universiteit van Amsterdam.

Říčan O., Piálek L., Dragová K. & Novák J. 2016. Diversity and evolution of the Middle American cichlid fishes (Teleostei: Cichlidae) with revised classification. *Vertebrate Zoology* 66 (1): 1–102. https://doi.org/10.3897/vz.66.e31534

Říčan O., Almirón A. & Casciotta J. 2017. Rediscovery of *Crenicichla yaha* (Teleostei: Cichlidae). *Ichthyological Contributions of Peces Criollos* 50: 1–8.

Říčan O., Dragová K., Almirón A., Casciotta J., Gottwald J. & Piálek L. 2021a. MtDNA species-level phylogeny and delimitation support significantly underestimated diversity and endemism in the largest Neotropical cichlid genus (Cichlidae: *Crenicichla*). *PeerJ* 9: e12283. https://doi.org/10.7717/peerj.12283

Říčan O., Říčanová Š., Almirón A., Casciotta J. & Piálek L. 2021b. Parallel evolution of a new sympatric species pair of *Crenicichla* (Teleostei: Cichlidae) from Misiones, Argentina with a review of biogeography and mitonuclear discordance in the *C. mandelburgeri* species complex. *Journal of Zoological Systematics and Evolutionary Research* 59 (8): 2134–2149. https://doi.org/10.1111/jzs.12566

Taylor W.R. & Van Dyke G.C. 1985. Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study. *Cybium* 9: 107–119.

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Appendix. Comparative material.

Comparative material constitutes specimens examined in Casciotta *et al.* (2010, 2013), Piálek *et al.* (2010), and Piálek *et al.* (2015, 2019b). In addition, the following material, all from Argentina except otherwise noted, was studied. Repository abbreviations: FMNH = Field Museum of Natural History; MACN = Museo Argentino de Ciencias Naturales; MLP = Museo de La Plata; MSNG = Museo Civico di Storia Naturale di Genova, Italy.

Crenicichla iguassuensis Haseman, 1911

BRAZIL • holotype, 137.0 mm SL; Iguaçu River, Porto União da Victoria; FMNH 54159.

Crenicichla jupiaensis Britski & Luengo, 1968

ARGENTINA • 2 ex., 87.7–93.0 mm SL; Corrientes, Paraná River at Yahapé; MLP 11294.

Crenicichla lepidota (Heckel, 1840)

ARGENTINA • 1 ex., 151.6 mm SL; Corrientes, Paraná River Basin, Isla Apipé Grande, Ituzaingó; MACN-ict 7275 • 1 ex., 98.4 mm SL; Formosa, Paraguay River Basin, Riacho de Oro; MACN-ict 4091 • 2 ex., 116.0–165.7 mm SL; Misiones, Represa Estación Experimental Cerro Azul; MACN-ict 3656.

Crenicichla ocellata (Perugia, 1897)

PARAGUAY • holotype, 257.5 mm SL; Paraguay, Puerto 14 de Mayo, Bahía Negra, Chaco Boreal; MSNG 33700.

Crenicichla semifasciata (Heckel, 1840)

ARGENTINA • 1 ex., 176.6 mm SL; Formosa, Paraguay River Basin, Riacho de Oro; MACN-ict 6239.

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