ISSN 0097-3157

Proceedings of the Academy of Natural Sciences of Philadelphia 167: 69-86 2020

Cichla cataractae (Cichliformes: Cichlidae), new species of peacock bass from the Essequibo Basin, Guyana and Venezuela

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ABSTRACT.—A new species of peacock bass, *Cichla cataractae*, is distinguished from all congeners by molecular evidence and unique patterns of adult and juvenile pigmentation. Juveniles (<150 mm SL) have sides of body dominated by a series of three (sometimes four) dark blotches with the one below soft dorsal fin largest, attenuated posteriorly (long teardrop shape) but distinctly separated from elliptical caudal blotch; same blotches eventually with pale border (ocellated) in largest juveniles. Adult pattern on sides dominated by two distinct dark blotches, each one ocellated; anterior blotch rounded, located below anterior base of spinous dorsal fin and not extending above anterior lateral line; posterior blotch highly irregular in shape, located below soft dorsal fin and displaced dorsally; additional dark blotch below posterior base of spinous dorsal fin generally absent or small, ocellated or not, and level with anterior blotch; vertical bars on sides generally absent or faint; postorbital stripe always present, highly broken into irregular series of dark spots, each one usually ocellated. *Cichla cataractae* is endemic to the Essequibo Basin where it typically inhabits rocky shoals in river channels with swift current. The new species is sympatric with the more widely distributed *C. ocellaris*, a species that prefers lentic habitats. Molecular analysis supports *C. cataractae* as a distinct lineage in a clade of *Cichla* containing *C. temensis*, *C. melaniae*, *C. mirianae*, *C. piquiti* and *C. pinima*. The oldest extant specimens of the new species were collected in by Carl H. Eigenmann in 1908 and documented in his seminal "The Freshwater Fishes of British Guiana" (Eigenmann, 1912).

Keywords: biodiversity, biogeography, freshwater, neotropical, taxonomy, systematics

New species: *Cichla cataractae* Sabaj, López-Fernández, Willis, Hemraj, Taphorn and Winemiller

Submitted: 18 Dec 2019, Accepted 24 Feb 2020.

INTRODUCTION

The earliest taxonomic accounts of *Cichla* in Guyana are attributable to Sir Robert Hermann Schomburgk (1804–1865) who explored much of the region during the years 1835–1839 and 1841–1844. During his first expedition, Schomburgk had drawings made of the fishes caught and added his own field notes to each one. Sir William Jardine (1800–1874) later edited the notes, assigned taxonomic names to the drawings, and published the "Fishes of British Guiana" in two parts (Schomburgk, 1841; 1843) as volumes III and V of "The Naturalists Library". The authorship of species described in those works is attributed to Jardine or to Jardine and Schomburgk, the latter better reflecting Schomburgk's conceptualization of the species, if not its Linnaean name. Because no type specimens exist, the taxonomic treatment of Jardine and Schomburgk's species is restricted to the published notes and color illustrations. Furthermore, many of the drawings are likely composites of multiple specimens (Eigenmann, 1912). Schomburgk (1841:82) noted that "the first specimen of any [undrawn] fish…served generally to sketch its outward forms and general colors on the paper; and when…fortunate enough to secure a second specimen those delicate hues were painted in, which are only visible immediately after the fish comes out of the water." As a result, some drawings show conflicting features that may be characteristic of more than one species.

From Schomburgk's notes and drawings, Jardine identified four species currently placed in the genus *Cichla* Bloch and Schneider 1801 (Fig. 1). He referred one to the nominal *Cichla argus*, a species described by Valenciennes in Humboldt and Valenciennes (1821). Kullander and Ferreira (2006) placed *C. argus* in the synonymy of *Cichla orinocensis* Humboldt 1821. Both species were described in the same work (Humboldt and Valenciennes, 1821) and *C. orinocensis* has priority by action of the first reviser, Günther (1862). Schomburgk (1843:149) noted his *C. argus* "in the Essequibo [Guyana] as well as in the Rios Branco and Negro [Brazil]"; however, its synonym *C. orinocensis* does not occur in the Essequibo basin. Schomburgk's illustration of *C. argus* (Fig. 1A) depicts three large round ocellated spots on the side of the fish, which is consistent with *C. orinocensis*, but not with any *Cichla* known from Guyana.

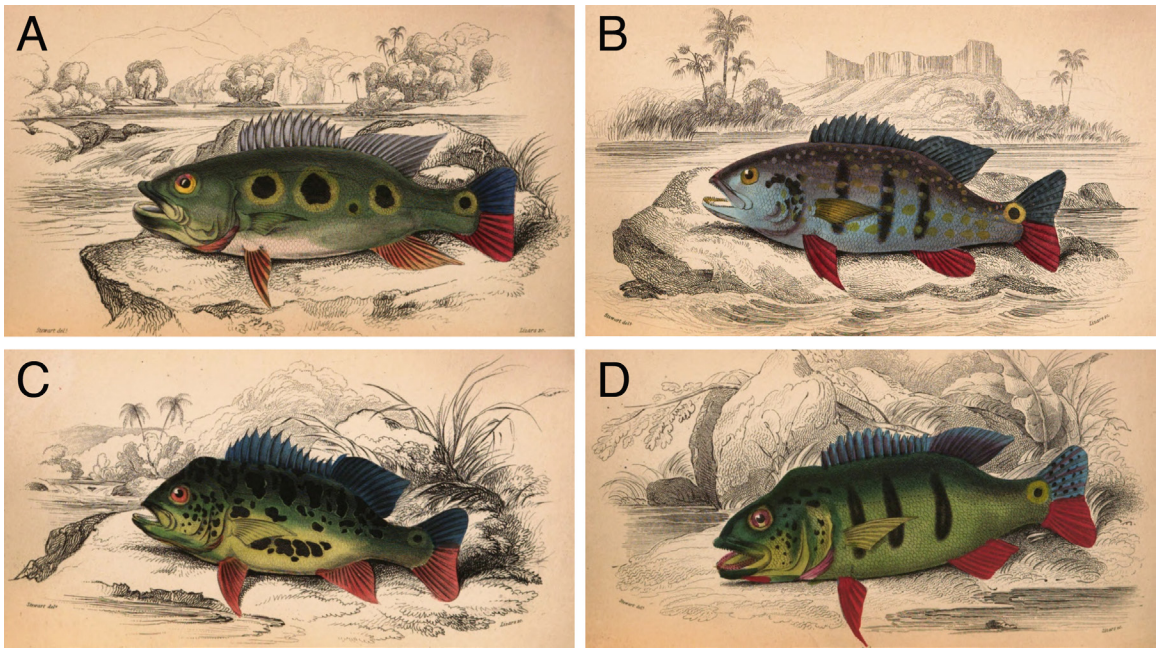


Fig. 1. Drawings of *Cichla* from Guyana and neighboring regions in Venezuela and Brazil as published in Schomburgk (1843). Scientific names assigned by William Jardine are followed by "Schomburgk Drawing" number, locality as published, and current status in parentheses. A. *Cychla argus*, Valenciennes? (No. 47): Essequibo as well as Rios Branco and Negro (synonym of *Cichla orinocensis* Humboldt 1821). B. *Cychla flavo-maculata* (No. 45): Rio Negro and Padauiri (synonym of *Cichla temensis* Humboldt 1821). C. *Cychla nigro-maculata* (No. 46): having same habits and residing in the same situations with the last [*C. flavo-maculata*] (synonym of *C. ocellaris* Bloch and Schneider 1801). D. *Cychla trifasciata* (No. 59): Rio Negro and in the Padauiri (synonym of *C. temensis* Humboldt 1821).

Jardine assigned new species names to the other three species of *Cichla* documented by Schomburgk: *C. flavomaculata*, *C. nigromaculata* and *C. trifasciata*. Schomburgk (1843:145) noted *C. flavomaculata* from the Negro River and its left-bank tributary the Padauiri, and *C. nigromaculata* as "residing in the same situations" (Schomburgk, 1843:147), leading one to believe the two were sympatric if not syntopic. Schomburgk (1843:151) similarly noted *C. trifasciata* from the Negro and Padauiri. Kullander and Ferreira (2006) placed *C. flavomaculata* and *C. trifasciata* in the synonymy of *C. temensis*, a species described in part from Temi in the upper Orinoco Basin by Humboldt in Humboldt and Valenciennes (1821). Schomburgk's (1843) illustration of *C. flavomaculata* (Fig. 1B) depicts a fish with three black vertical bars and horizontal rows of yellow spots on its side. Among *Cichla* species in the Negro Basin, only *C. temensis* shares this color pattern and has priority as the older name. Schomburgk's (1843) depiction of *C. trifasciata* also has three black vertical bars, but it lacks the rows of pale spots (Fig. 1D). The illustrated fish is evidently a breeding male due to its enlarged nuchal hump. Large male and female *C. temensis* lose their light spots when in breeding condition and otherwise resemble Schomburgk's drawing of *C. trifasciata*. Most records for *C. temensis* are from black and clear water rivers in the Orinoco and Negro drainages (Kullander and Ferreira, 2006), the latter including the Pirara River, a small tributary in the upper Branco basin (Lowe-McConnell, 1969; Willis et al., 2015).

Kullander and Ferreira (2006) considered Schomburgk and Jardine's fourth *Cichla*, *C. nigromaculata*, to be a valid species endemic to the upper Orinoco, Casiquiare and middle Negro basins. They distinguished *C. nigromaculata* from its putative sister species *C. ocellaris* Bloch and Schneider 1801 by a variety of characteristics including postorbital markings absent (vs. present), occipital bar distinct (vs. absent or indistinct), dark vertical bars wide dorsally, tapering ventrally (vs. width more uniform), dorsal side with small black spots, lateral line discontinuous (vs. usually continuous), 75–84 (vs. 67–82) scales in E1 row, and caudal peduncle narrower, depth 10.3–11.4% SL (vs. 11.9–13.2% SL) in specimens >100 mm SL. Alternatively, Willis et al. (2012) disputed the species-level validity of *C. nigromaculata* based on molecular data. According to their analysis, mtDNA haplotypes of *C. nigromaculata* nested within those of *C. monoculus* Agassiz 1831, and microsatellites grouped *C. nigromaculata* with *C. ocellaris* and *C. monoculus*. They considered *C. nigromaculata*, *C. monoculus* and two other nominal species to be members of an expanded concept of *C. ocellaris*.

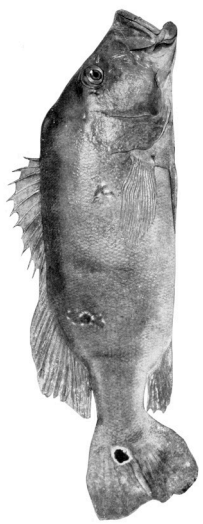
The taxonomic treatment of *C. nigromaculata* by Willis et al. (2012) echoed that of Carl Eigenmann a century beforehand. Faced with placing names on *Cichla* specimens from Guyana, Eigenmann (1912) tentatively referred all of his material to *C. ocellaris*, and he relegated to its synonymy the four *Cichla* species documented by Jardine and Schomburgk (Schomburgk, 1843). Eigenmann (1912:509) left "in abeyance the question whether or not there are two species of *Cichla* in [Guyana] and also the name by which they ought to be called". In fact, Eigenmann collected two species of *Cichla* during his expedition to Guyana in 1908 (Eigenmann, 1912; Hardman et al., 2002), one of which is described here as new based in part on his specimens.

With regards to nominal *Cichla* from Guyana, an additional taxon warrants brief mention. *Acharnes speciosus* was named by Müller and Troschel (1849) based on material from the coast and in the estuary of the Essequibo River collected by Richard Schomburgk (Robert's brother) during the 1841–1844 expedition. Subsequent authors (e.g., Eigenmann, 1912; Kullander and Ferreira, 2006) placed *Acharnes speciosus* in the synonymy of *C. ocellaris*.

Recent fieldwork in Guyana yielded additional specimens of the undescribed *Cichla* from upland habitats in the Essequibo River and its tributaries (e.g., Cuyuní, Rupununi). The new species was previously figured by Eigenmann (1912: Pl. 69) as *Cichla ocellaris* and by Kullander and Ferreira (2006:313, Fig. 20) as *Cichla* cf. *orinocensis*. Recognized by local fishermen as the "Falls Lukunani", the new species is strongly associated with rocky shoals in flowing channels of clear-water rivers, whereas the nominal *C. ocellaris* is found in a variety of habitats including backwaters and floodplain lakes. The objective of this study is to formally name and describe the Falls Lukunani and to provide comparisons to related and similar-looking species.

MATERIAL AND METHODS

Morphological Analysis.—Measurements and counts follow Kullander (1986) and Kullander and Nijssen (1989). All measurements taken point to point with digital calipers. Standard length (SL) measured from tip of upper jaw to middle of caudal-fin base. Count of scales in E1 row refers to scales in the horizontal row immediately above the scale row containing the lower lateral line. Vertebral counts were taken on X-rays and include the last half centrum; the first caudal vertebrae bears the first haemal spine, which normally coincides with the first haemal arch, and in *Cichla*, is usually posterior to the first anal-fin pterygiophore. Descriptions of color patterns include references to numeric codes proposed by Kullander and Ferreira (2006; abbreviated "K&F") for principal dark markings along the side of the body in *Cichla*, as well as rays in the dorsal (D) and ventral (V) lobes of the caudal fin.



C. ocellaris (kelberi), Araguaia, 1A
C. ocellaris (kelberi), Araguaia, 1B
C. ocellaris (kelberi), Tocantins, 2A
C. ocellaris (kelberi), Tocantins, 2B
C. ocellaris (monoculus), low. Tapajós, 1A
C. ocellaris (monoculus), mid. Tapajós, 1A
C. ocellaris (monoculus), mid. Tapajós, 1B
C. ocellaris (monoculus), low. Tapajós, 1B
C. ocellaris (pleiozona), Abunã, 1A
C. ocellaris (pleiozona), Abunã, 1B
C. ocellaris (pleiozona), Mamoré, 1A
C. ocellaris (pleiozona), Mamoré, 1B
C. ocellaris (monoculus), Tefé, 1A
C. ocellaris (monoculus), Nanay, 1A
C. ocellaris (monoculus), Nanay, 1B
C. ocellaris (monoculus), Tefé, 1B
C. ocellaris (monoculus), low. Jari, 1A
C. ocellaris (monoculus), low. Jari, 1B
C. ocellaris (monoculus), Araguari, 1A
C. ocellaris (monoculus), Araguari, 1B
C. ocellaris (monoculus), low. Xingu, 1A
C. ocellaris (monoculus), low. Xingu, 1B
C. ocellaris (monoculus), low. Negro, 1A
C. ocellaris (nigromaculata), up. Negro, 1A
C. ocellaris (nigromaculata), up. Negro, 1B
C. ocellaris (monoculus), low. Negro, 1B
C. ocellaris (monoculus), Unini, 1A
C. ocellaris (monoculus), Unini, 1B
C. ocellaris, Rupununi, 1A
pond lukunani, HLF1221A
pond lukunani, HLF824A
pond lukunani, HLF825A
pond lukunani, HLF1230A
pond lukunani, HLF1222A
pond lukunani, HLF1222B
C. ocellaris, Rupununi, 2A
C. ocellaris, Rupununi, 2B
pond lukunani, HLF1221B
pond lukunani, HLF1230B
pond lukunani, HLF847A
pond lukunani, HLF846A
pond lukunani, HLF846B
pond lukunani, HLF847B
pond lukunani, HLF825B
C. ocellaris, Takutu, 1A
C. ocellaris, Takutu, 2A
C. ocellaris, Takutu, 1B
C. ocellaris, Takutu, 2B
pond lukunani, HLF824B
C. ocellaris, Rupununi, 1B
pond lukunani, HLF616A
pond lukunani, HLF616B
C. cf. ocellaris, Marowijne, 1A
C. cf. ocellaris, Marowijne, 1B
unknown, Suriname, HLF353A
unknown, Suriname, HLF354A
unknown, Suriname, HLF353B
unknown, Suriname, HLF354B
unknown, Cosewijne, HLF001A
unknown, Cosewijne, HLF001B
C. orinocensis, Cinaruco, 1A
C. orinocensis, Atabapo, 1A
C. orinocensis, Atabapo, 1B
C. orinocensis, Unini, 1A
C. orinocensis, Unini, 2A
C. orinocensis, Unini, 1B
C. orinocensis, Unini, 2B
C. orinocensis, Cinaruco, 1B
C. intermedia, Ventuari, 1A
C. intermedia, Ventuari, 1B
C. intermedia, Caura, 1A
C. intermedia, Caura, 1B
100
100
100
100
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100
92
100
100
100
100
100
100
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100

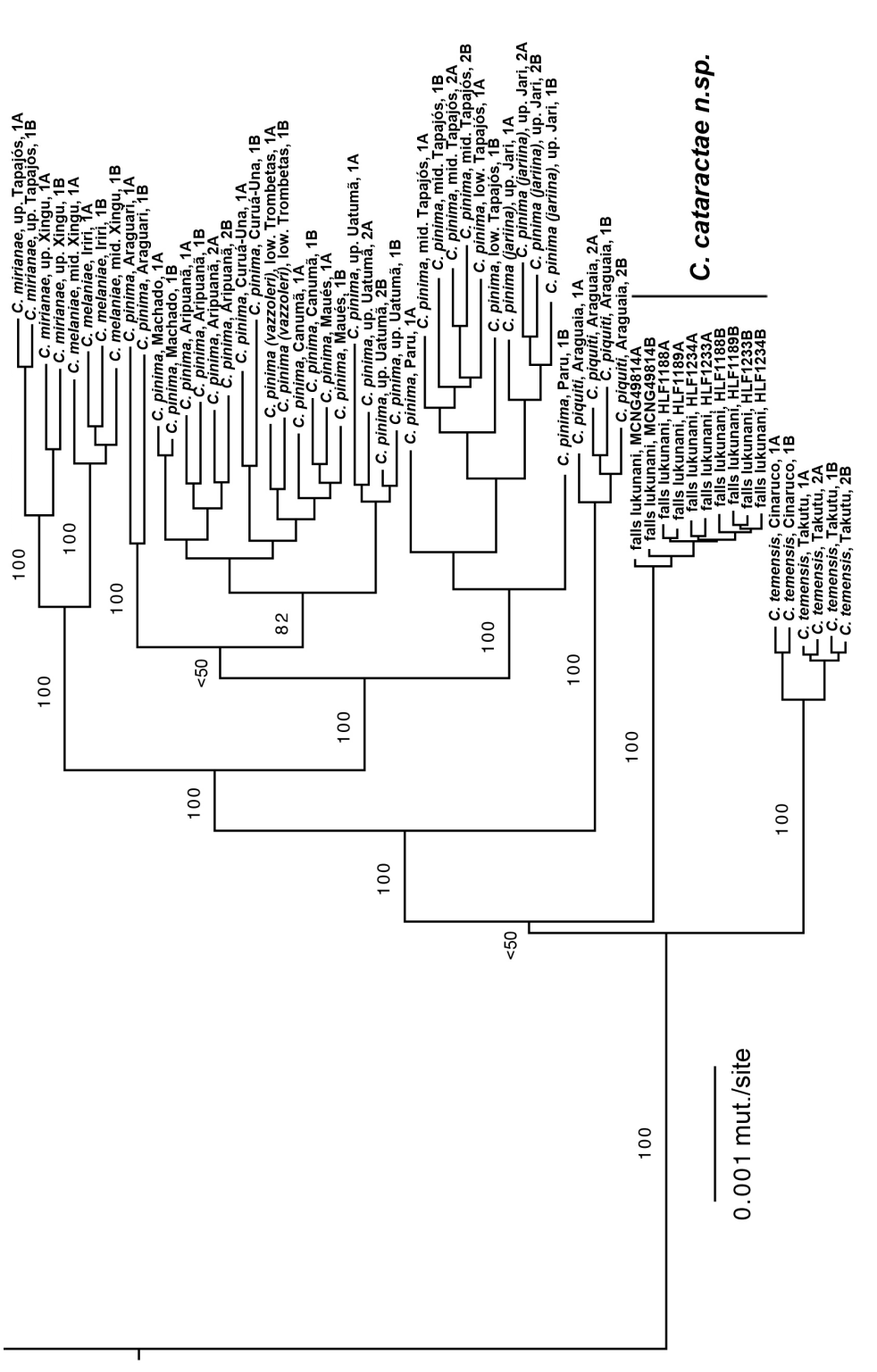


Fig. 2. Phylogenetic placement of *Cichla cataractae*, n. sp. (Falls Lukunani), based on maximum likelihood analysis of DNA sequence data (see Results section). Terminals named according to Willis et al. (2012: Table 3) followed by species names used by Kullander and Ferreria (2006) in parentheses when different. HLF1188 refers to voucher CSBD F 3613 (holotype); HLF1189, HLF1233 and HLF1234 refer to vouchers UMMZ 250942 (paratypes). Each individual represented by two terminal branches (e.g., "1A" and "1B") corresponding to two diploid sequences (i.e., randomly concatenated phased haplotypes from many loci on several chromosomes). Inset: Large male *Cichla cataractae*, n. sp. (Eigenmann 1912: Plate 69, Fig. 4).

Species-level taxonomy follows recommendations of Willis et al. (2012: Table 3) that synonymize nominal *Cichla jariina*, *C. thyrorus* and *C. vazzoleri* into an expanded concept of *C. pinima*, and *C. kelberi*, *C. monoculus*, *C. nigromaculata* and *C. pleiozona* into an expanded *C. ocellaris*. A more formal synonymization of those taxa is beyond the scope of this paper. Furthermore, the alternative treatment of those taxa as valid (i.e., Kullander and Ferreria, 2006) does not affect the diagnosis of the new species described here or its recognition as an independent, species-level taxon in *Cichla*. Institutional codes follow Sabaj (2019).

Molecular Analysis.—Tissues were sampled from specimens of *Cichla* from Guyana to assess the distinctiveness of the new species and its placement in the genus. Alongside specimens previously utilized in Willis et al. (2012), novel and extensive molecular data were collected from over one thousand nuclear regions using a double digest restriction site associated procedure (ddRAD) modified from Peterson et al. (2012). DNA was extracted from tissue using the Mag-Bind HDQ DNA extraction kit (Omega), digested with enzymes EcoRI and SphI (New England Biolabs), ligated to barcoded DNA adapters (Peterson et al., 2012), pooled equimolarly and size selected to 250–500 base pairs using a Pippin Blue 1.5% dye-free agarose cassette (Sage Science), amplified using Phusion polymerase (New England Biolabs) with one of four indexed primers, and sequenced on the Illumina HiSeq 4000. Sequence data were processed using the dDocent pipeline v2 (Puritz et al., 2014) including construction of a pseudo-reference using sequences observed at least five times within an individual (K1), three times across all individuals (K2), and clustered at minimum of 80% sequence similarity (c). Final filtering thresholds using VCFtools (Danecek et al., 2011) and vcflib (Garrison, 2014) included a minimum Phred quality of 30, minimum genotype depth of 5 reads, maximum individual missingness of 50%, and maximum locus missingness of 10% (O'Leary et al., 2018). Only bi-allelic SNPs were retained, and paralogs were filtered following Willis et al. (2017), from which haplotypes (two per individual) at each contiguous nuclear region were produced for 8,495 fragments. Markers were further filtered as only those matching the expectations of the infinite sites model (Kimura, 1969), which predicts no more than one haplotype greater than the number of SNPs in a contiguous sequence, thus excluding recombinants. From these, only fragments with ten or more variable sites (n = 1,230) were retained for phylogenetic analysis to maximize the information content of the alignment relative to computational time.

Sequence data were concatenated for analysis, and the haplotypes from each individual were randomly combined to test for any major effects of incomplete lineage sorting or introgression on topological inference (two concatenated sequences per individual). Using jModeltest (Posada, 2008), the HKY+I+G was selected as optimal, followed by the GTR+I+G model (data not shown). This was implemented in RaxML v8 using the GTRGAMMA option (Stamatakis, 2014), with 100 bootstrap replicates; other parameters were left as default, and the data were treated as a single partition.

RESULTS

Molecular Analysis.—The DNA sequence alignment consisted of 356,379 sites, of which 15,370 were variable and 12,894 were parsimony informative. The maximum likelihood analysis supported the same general relationships within *Cichla* previously discussed by Willis et al. (2007; 2010; 2012; 2013; 2015) and Willis (2017). The alpha-level diversity of *Cichla* is divided into two clades, A and B, composed of six and three species, respectively. Individuals from the Essequibo Basin identified as the new species *Cichla cataractae* (Falls Lukunani) were recovered as one of the lineages in Clade A, and there is weak support for a sister-group relationship with a clade containing *C. melaniae*, *C. mirianae*, *C. piquiti*, and *C. pinima* (but see Willis et al., 2017). Individuals from the Essequibo Basin putatively identified as *C. ocellaris* (Pond Lukunani) were placed in Clade B. Those individuals grouped with samples from Willis et al. (2012) previously identified as *C. ocellaris*, and in a larger clade containing nominal *C. monoculus*, *C. kelberi*, and *C. pleiozona*, referred to collectively as *Cichla ocellaris sensu lato* (Willis et al. 2012). Similarly, samples from the Suriname and Marowijne grouped within this larger *C. ocellaris sensu lato* clade, along with previous Marowijne samples of *C. aff. ocellaris* analyzed by Willis et al. (2012).

***Cichla cataractae*, new species**

Falls Lukunani

Figs. 3–5

Cichla ocellaris.—Eigenmann 1912 [in part; p. 510, one specimen from Tumatumari, one from Warraputa, two from Gluck Island, and at least 139 specimens from Rockstone; plate 69, fig. 1 of young, 50 mm (CM 2281), fig. 2 of young, 138 mm (CM 2279), fig. 4 of adult, 660 mm, from photo taken in field].—Román 1981: 104 [in part; presumably locality plotted on río Cuyuní near Anacoco Island on distribution map for *Cichla* in Venezuela].—Watkins, et al. 2004 [in part; checklist of fishes from Iwokrama Forest, Guyana].

Cichla cf. *orinocensis*.—Kullander and Ferreira 2006:307, 313 [material examined and figure 20 of MBUCV-V 10287, 82.3 mm SL, from río Cuyuní, Venezuela].

Holotype.—CSBD F 3613, tag T01188 [ex. UMMZ 250942] (308.0 mm SL, female). Guyana: Rupununi River off of Manaho Lagoon, 3°59'33.8"N 58°44'45.8"W, H. López-Fernández, D.C. Taphorn, K.O. Winemiller, D.D. Bloom, S.E. Steele, T.D. Morgan, K. Foster and S. Anderson, 18 Apr 2018.

Paratypes (159).—All Guyana: AMNH 214977 (1, 140.9 mm SL), Essequibo River at Rockstone, A.S. Pinkus, 1935; ANSP 176029 (1, 137.7 mm SL), Essequibo River, approx. 3 hours upstream from Kurupukari field station, 4°34'17"N, 58°35'17"W, W.G. Saul et al., 30 Jan 1997; ANSP 177095 (1, 86.4 mm SL), ANSP 177096 (1, 55.3 mm SL), Burro Burro River, Water Dog Falls (camp), 4°40'48"N, 58°50'54"W, G. Watkins et al., 18 Nov 1997; ANSP 177097 (3, 38.5, 42, 60.7 mm SL), Burro Burro River, Water Dog Falls (camp), Station 4A, 4°40'48"N, 58°50'46"W, G. Watkins et al., 19 Nov 1997; ANSP 177098 (1, 44.3 mm SL), Essequibo River, extensive sandbar 2.0 km upstream from Paddle Rock campsite, 4°42'20"N, 58°42'26"W, C. Watson et al., 25 Nov 1997; ANSP 177100 (1, 104.0 mm SL), CSBD F 849 (1), Essequibo River, rock landing, 4°44'22"N, 58°42'23"W, C. Watson et al., 24 Nov 1997; ANSP 205693 (3, 26.4, 27.6, 27.9 mm SL), CSBD F 3612 (1), Essequibo River, sand bar some 50 minutes upstream from Kurupukari field station, 4°42'47"N, 58°42'40"W, W.G. Saul et al., 27 Jan 1997; AUM 72123 (1, 107.0 mm SL), CSBD F 837 (1), Essequibo River, rocky area 200 m downstream from Paddle Rock campsite, 4°44'23"N, 58°42'42"W, D. Torres et al., 23 Nov 1997; CAS 20727 (1, 98 mm SL), FMNH 53782 (1, 110.5 mm SL) [both ex CM 2279/IU 12452], Gluck Island, 29 Sep–2 Oct, C.H. Eigenmann & party; CAS 20729 (28, 39.0–43.7 mm SL), CAS 21852 (5, 37.8–43 mm SL), FMNH 7543 (5, 37.8–42.5 mm SL), FMNH 53784 (9, 39.3–42 mm SL), FMNH 69680 (85, 31.8–44.5 mm SL), MCZ 30130 (4 extant, 39.1–42.9 mm SL) [all ex CM 2281/IU 12454], Rockstone Stelling, 29 Sep–2 Oct, C.H. Eigenmann & party; FMNH 53779 (1, ~600 mm TL; specimen lacking internal organs, axial skeleton and musculature) [ex CM 2277/IU 22450], Potaro River at Tumatumari, 7–9 Oct 1908, C.H. Eigenmann & party; FMNH 53785 (1, 93.6 mm SL) [ex CM 2282], Essequibo River at Warraputa Falls, C.H. Eigenmann & party, 6 Nov 1908; UMMZ 215816 (1, 100.2 mm SL), Mazaruni River, at hill top and in small creek (rainy season), 5°47'41.3"N 59°37'40.7"W, D. Cichocki & Carlson, 25 Aug 1971; UMMZ 250942 (3, 365–384 mm SL), same data as holotype.

Non-types (4).—Guyana: FMNH ex. 53784 [ex CM 2281/IU 12454] (3 cs), Rockstone Stelling 29 Sep–2 Oct, C.H. Eigenmann and party. Venezuela: Bolívar: MBUCV-V 10287 (1, 82.3 mm SL), río Cuyuní, raudal de Kinotovaca, ca. 40 km south of El Dorado, F. Mago Leccia, 22 Jan 1977.

Diagnosis.—*Cichla cataractae*, n. sp., is distinguished from all congeners by unique aspects of coloration (Figs. 3–5). In juveniles (<150 mm SL), pattern on sides of body generally dominated by series of three prominent dark blotches. Anterior one below anterior base of spinous dorsal fin (K&F marking 1); posterior one below soft dorsal fin (K&F markings 2a to 4); caudal blotch spanning rear margin of peduncle and finishing on base of middle caudal-fin rays

Fig. 3. *Cichla cataractae*, Holotype, CSBD F 3613, tag T01188 [ex. UMMZ 250942] (308.0 mm SL, female). Guyana: Rupununi River off of Manaho Lagoon, 3°59'33.8"N 58°44'45.8"W. Photo by HLF.

(between V3 and D3 of K&F); smaller fourth dark blotch sometimes present below posterior base of spinous dorsal fin (K&F marking 2). Dark blotch below soft dorsal fin largest, deeper anteriorly and tapered posteriorly to about mid-length of caudal peduncle (long teardrop shape), but kept separate from elliptical caudal blotch. In adults, lateral pattern dominated by two prominent dark blotches, each one with pale border (ocellated markings of K&F). Anterior ocellated blotch (K&F marking 1) rounded, located below anterior third of spinous dorsal fin, and not extending above anterior portion of lateral line; secondary dark marking sometimes present below and separate from main anterior one, vertically elongated and sometimes ocellated, its appearance obscured beneath folded pectoral fin (Fig. 5B). Posterior ocellated blotch (K&F marking 3) located below soft dorsal fin and displaced dorsally (i.e., ventral border finishing above posterior portion of lateral line); highly irregular in shape, sometimes broken into row of ocellated markings that decrease in size caudally. Additional dark marking below posterior base of spinous dorsal fin (K&F marking 2) generally absent or small, ocellated or not, and horizontally aligned with anterior marking. Vertical bars on sides generally absent or faint. Postorbital stripe present; in adults, stripe highly broken into irregular series of dark spots, each one usually ocellated. Lateral line bilaterally continuous.

Comparisons.—In others species of *Cichla*, the juvenile pattern is dominated either by a dark midlateral stripe that is more or less continuous from cleithrum to end of caudal peduncle (*C. intermedia, C. melaniae, C. mirianae, C. pinima, C. piquiti* and *C. temensis*), or by three dark vertical bars (or blotches) located below the anterior and posterior bases of the spinous dorsal fin and soft dorsal fin, respectively, the lattermost one connected to the caudal blotch via dark midlateral stripe (*C. ocellaris* and *C. orinocensis*). Juveniles of *C. cataractae* most closely resemble those of *C. ocellaris* (Fig. 4) and *C. orinocensis* by having a 2–3 similarly placed dark markings. But, the enlarged dark marking below the soft dorsal fin is distinctly separate from the caudal blotch in all juveniles examined for *C. cataractae* (vs. connected via dark stripe in *C. ocellaris* and *C. orinocensis*).

The adult pattern in *Cichla* is highly variable, but only a few species have sides with large ocellated blotches (*C. orinocensis* and sometimes *C. mirianae* and *C. pinima*), and those species typically have three (vs. two, middle one generally missing in *C. cataractae*). Furthermore, the three ocellated blotches in *C. mirianae* and *C. pinima*, when present, are often vertically elongated or otherwise accompanied by additional ocellated markings above and below.

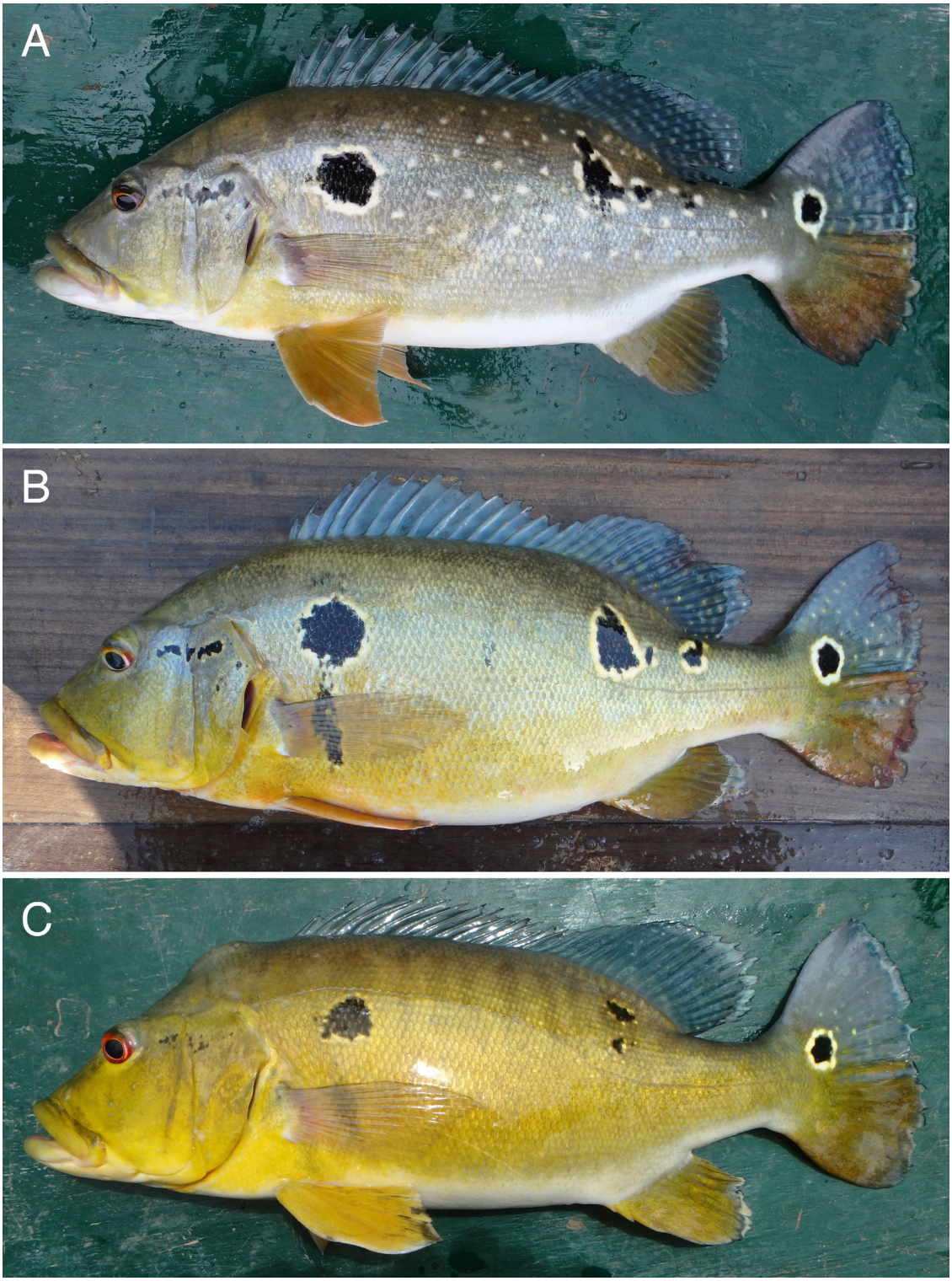
Cichla ocellaris is sympatric with *C. cataractae* in the Essequibo Basin, and adults often share the presence of an ocellated blotch below the soft dorsal fin. However, *C. ocellaris* generally has 2–3 dark vertical bars that reach the anterior and posterior base of the spinous dorsal fin and base of soft dorsal fin, respectively (each bar appears as an elongated inverted triangle pointed ventrally; Figs. 4H, 6), vs. two ocellated blotches similarly aligned to anterior spinous and soft dorsal fin, respectively, but not reaching dorsal-fin base in *C. cataractae*. *Cichla ocellaris* occasionally has three rounded ocellated blotches similarly aligned to the dorsal fin; but the two anterior-most ones are located more dorsally than in *C. cataractae* (e.g., first dark blotch mostly above anterior lateral-line in *C. ocellaris* vs. entirely below in *C. cataractae*). Furthermore, adult and juvenile *C. cataractae* have dark postorbital markings (vs. dark markings absent from head in *C. ocellaris*), and adult *C. ocellaris* almost always have a longitudinal series of dark abdominal blotches on lower anterior sides (vs. absent or restricted to single, vertically elongated blotch in *C. cataractae*).

Cichla cataractae also has a bilaterally continuous lateral line which helps distinguish it from species with lateral line usually or always discontinuous (*C. melaniae, C. mirianae, C. orinocensis* and *C. piquiti*; Kullander and Ferreira, 2006). *Cichla ocellaris* from Guyana also have a discontinuous lateral line (Figs. 4G–H, 6; J. Armbruster, pers. comm. 2020), although Kullander and Ferreira (2006:303) described the lateral line of this species as "usually continuous" based on specimens ranging from northeastern Venezuela to French Guiana.

Description.—See Figs. 3–5 for shape and color pattern; Table 1 for morphometrics and meristics. *Cichla cataractae* is a moderately-sized member of its genus known to reach ~600 mm TL (FMNH 53779) and 660 mm TL based on fish preserved and figured, respectively, by C.H. Eigenmann (1912) (see also Ecology section).

Body laterally compressed and moderately deep; depth at vertical through pelvic-fin origin 26.5–29.6% of SL in specimens 104.0–137.7 mm SL (n=4) and 32.5–34.6% of SL in adults 308.0–384.0 mm SL (n = 4). Mouth large, wide, low and terminal in position. Lower jaw prognathous, its articulation below the anterior half of orbit when mouth fully closed. Dorsal profile of head straight, rising at about 45° angle from snout tip to vertical through posterior margin of preopercle, but steeper in mature males with nuchal hump beginning near vertical through anterior margin of preopercle; then curved to dorsal-fin origin, straight to slightly convex to end of spinous dorsal-fin, then descending steeply to caudal peduncle and straight to caudal-fin base. Nuchal hump

Fig. 4. Juvenile specimens of *Cichla cataractae*, n. sp. (A–F) and *Cichla ocellaris* (G–H) from Guyana. A. ANSP 205693 (27.9 mm SL). B. ANSP 177097 (42 mm SL). C. ANSP 177097 (60.7 mm SL). D. ANSP 177095 (86.4 mm SL). E. ANSP 177100 (104.0 mm SL). F. ANSP 176029 (137.7 mm SL). G. ANSP 176032 (37 mm SL). H. CAS ex. 20729 (144.5 mm SL). A, E, F, G from Essequibo River upstream of Kurupukari; B–D from Burro Burro River, Water Dog Falls; H. from Essequibo River at Rockstone. Scale bar = 1 cm. Photos by MHS.


A
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C

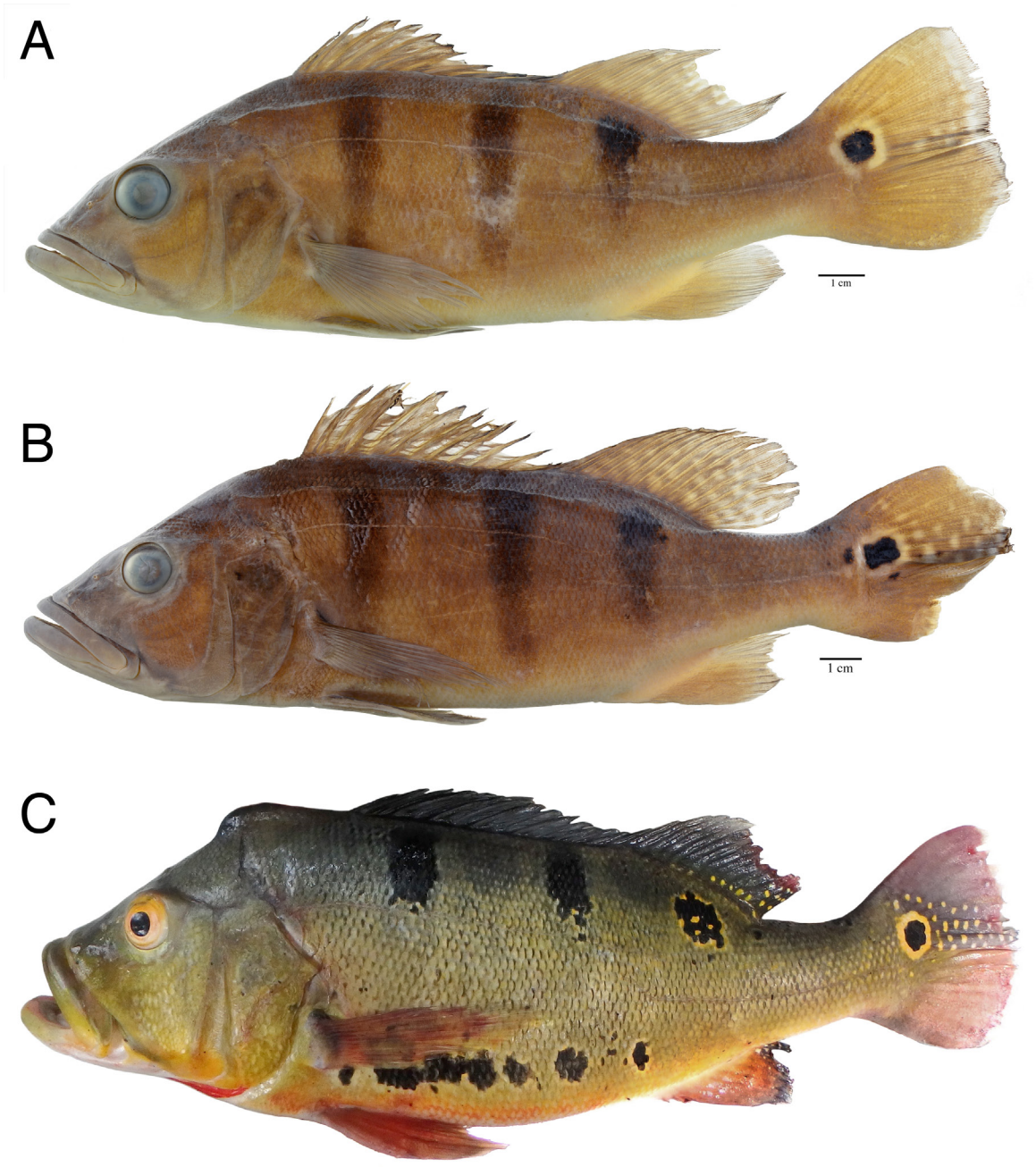

Fig. 6. (above) *Cichla ocellaris*. Subadult specimens from Essequibo River, 4°45'41" N, 58°45'53"W (A–B) and fresh dead breeding male from lower Rupununi River, Essequibo Drainage (C), Guyana. A. ANSP 176028 (178 mm SL). B. ANSP 176030 (205.3 mm SL). Scale bar = 1 cm. Photos by MHS (A, B) and KOW (C).

Fig. 5. (Page 78) Adults of *Cichla cataractae*, n. sp., all captured from same rocky shoals in Rupununi River, Essequibo Drainage, Guyana. A. female (CSBD F 3613, holotype, 308 mm SL). B. likely gravid female (UMMZ 250942, paratype, 369 mm SL). C. breeding male with nuchal hump and bright red eye (UMMZ 250942, paratype, 365 mm SL). Photos by KOW.

observed in male 365.0 mm SL (UMMZ 250942). Ventral profile flat to slightly descending to quadrate articulation; lower lip fold discontinuous at symphysis. Jaw teeth small, recurved, arranged in four to eight irregular rows that form patches separated by a distinct symphyseal gap in both upper and lower jaws.

Lateral scales ctenoid, becoming weakly ctenoid distally on caudal fin. Preopercle naked; opercle fully scaled, scales cycloid to weakly ctenoid; subopercle and cheek densely scaled, cycloid; interopercle posteriorly scaled, cycloid. Scales on sides of body small, becoming slightly larger ventrally. Scales along middle of side (E1 scale row) 79–83. Lateral line bilaterally continuous in eight specimens examined (100.2–384.0 mm SL). Lateral line continued onto caudal fin by a few scales; dorsal extension of lateral line on upper lobe between rays D3–D4. Lateral-line scales on body approximately equal in size to adjacent scales. Prepelvic and chest scales extremely small except posteromedial ones; posteromedial scales approximating size of flank scales. Scales absent above orbits; predorsal squamation reaching rostrad almost to anterior orbital margin. Scales absent from predorsal midline area except for narrow, irregular patch from about mid-orbit to nuchal hump in only dimorphic male available for examination. Dorsal fin naked; anal fin with basal sheath of cycloid scales; pectoral and pelvic fins naked except for a few scales near base on distal side.

Abdominal + caudal vertebrae: 17 + 18 = 35 total (n = 4), 17 + 19 = 36 total (1). Dorsal-fin spines modally 15 (6), 14 in one adult from Rupununi River and 12 in juvenile (100.2 mm SL) from Mazaruni River; spines increasing in length to sixth or seventh, then gradually decreasing to end of spinous portion. Soft dorsal-fin rays modally 17, range 16–18 (8); soft-rayed portion of dorsal fin about as high as anterior spinous portion, longest rays 11th or 12th, reaching posteriorly to dorsal procurrent caudal-fin rays in adults vs. middle of peduncle in juveniles. Anal fin with three spines and modally 11 soft rays, range 10–12 (8); anal fin large, distally rounded, rays reaching ventral procurrent rays of caudal fin in large specimens, otherwise to ½–¾ of peduncle length. Pelvic fin with anterior spine and five branched rays; spine inserted slightly anterior to or aligned with vertical through pectoral-fin base; fin shape subacuminate with medial rays gradually shorter; distal tip formed by rays 1–2, finishing less than halfway to anal-fin origin in juveniles and females, halfway in mature males. Pectoral-fin rays modally 14, range 13–16 (8); fin shape acuminate with rays 4 or 5 longest in adults; distal tip finishing between ½ and ¾ distance between fin insertion and anal-fin origin, slightly to clearly beyond vertical through tip of folded pelvic fin. Caudal fin with 16 principal rays, eight in each lobe; posterior margin emarginate in juveniles, gently convex in adults (edge often ragged).

Color in alcohol.—All juvenile stages share lateral series of three prominent dark blotches: anterior, posterior and caudal (Figs. 4A–F). Anterior one located below anterior base of spinous dorsal fin (K&F marking 1); posterior one below base of soft dorsal fin and extends onto anterior portion of caudal peduncle (K&F markings 2a to 4); caudal blotch begins on terminus of peduncle and finishes on base of middle caudal-fin rays. Some specimens with additional small dark central blotch below posterior base of spinous dorsal fin (K&F marking 2).

In small juveniles (<40 mm SL; Fig. 4A), anterior and caudal blotches rounded and posterior one horizontally elongated; none ocellated. Broader, less-intensely pigmented (dusky) marking alongside the base of spinous dorsal fin and situated directly above, but separate from anterior blotch. Dusky postorbital stripe evident; occipital bar absent. Chin, snout and dorsal portions of head and body dusky; undersides and fins mostly pale.

In larger juveniles (ca. 40–60 mm SL; Figs. 4B,C), posterior dark blotch (below soft dorsal fin) more elongated and tapered posteriorly (long teardrop shape), but kept separate and distinct from caudal blotch. Small dark central blotch (K&F marking 2) often added to lateral series below posterior base of spinous dorsal fin. Faint dusky vertical bars often associated with anterior and central blotches, respectively, as well as anterior portion of posterior (teardrop-shaped) one. Dusky blotch alongside spinous dorsal-fin base expanded longitudinally. Postorbital bar becoming more distinct, continuous; dusky preorbital bar evident. Background color becoming slightly darker, but still well contrasted with dark markings. Spinous dorsal fin and anterior portion of soft dorsal fin with patches of dark pigmentation; remaining fins mostly pale, hyaline.

In largest juveniles examined (86–137.7 mm SL; Figs. 4D–F), three prominent blotches in lateral series becoming ocellated (i.e., accented by distinct, pale border). Some individuals with irregular dusky stripe level with postorbital stripe and loosely joining anterior, central (when present), and posterior dark blotches. Caudal ocellus remains separate and placed midlaterally on terminus of caudal peduncle and base of middle caudal-fin rays. Faint vertical bars remain associated with anterior, central and posterior blotches, respectively (K&F markings 1, 2 and 3), and each interspace with fainter bar sometimes evident (K&F markings 1a and 2a). Dusky elongate blotch persists alongside base of spinous dorsal fin, and in one specimen (Fig. 4D), extends posteriorly to base of soft dorsal fin as darkened cloak. Pre- and postorbital bars distinct; dark narrow occipital bar evident in one specimen (Fig. 4D). Dorsal fin with dark pigment creating irregularly shaped pale windows. Caudal fin with dark pigment more uniformly distributed, although irregular pale areas evident in dorsal lobe of largest juveniles (Figs. 4E,F).

Table 1. Morphometrics and meristics of *Cichla cataractae*, n. sp. ND = not determined.

	Holotype	Paratypes (n=7)						All specimens			
	CSBD F 3614 (tag T1188)	UMMZ 215816	ANSP 177100	AUM 72123	ANSP 176029	UMMZ 250942 (tag T1189)	UMMZ 250942 (tag T1234)	UMMZ 250942 (tag T1233)	Range			SD
Standard length (SL) in mm	308.0	100.2	104.0	107.0	137.7	365.0	369.0	384.0	100.2	–	384.0	—
percent of SL												
Head length	33.8	33.7	34.8	34.1	32.7	35.2	33.1	35.4	32.7	–	35.4	0.98
Snouth length	12.1	11.5	14.5	14.1	12.3	11.8	10.9	11.8	10.9	–	14.5	1.28
Head depth	25.7	22.6	23.2	23.4	22.1	25.8	25.3	24.8	22.1	–	25.8	1.47
Body depth at pelvic origin	33.6	27.4	26.5	28.1	29.6	34.6	32.5	33.6	26.5	–	34.6	3.19
Orbit diameter	6.0	8.5	6.8	6.7	6.7	6.2	6.2	6.0	6.0	–	8.5	0.81
Interorbital width	9.0	8.0	8.6	8.4	8.9	9.0	9.2	9.4	8.0	–	9.4	0.46
Pectoral fin length	24.0	damaged	19.7	18.3	21.0	23.9	22.8	22.0	18.3	–	24.0	2.14
Upper jaw length	15.7	15.7	14.3	14.6	15.5	16.1	16.2	16.2	14.3	–	16.2	0.72
Lower jaw length	19.9	19.6	18.3	18.8	19.8	20.0	20.3	19.7	18.3	–	20.3	0.68
Caudal peduncle depth	13.1	11.4	10.4	10.7	10.9	12.3	11.7	12.7	10.4	–	13.1	0.98
Caudal peduncle length	16.3	17.5	17.3	18.7	16.9	15.2	18.6	17.7	15.2	–	18.7	1.18
Dorsal spine length	11.5	11.4	damaged	7.4	7.4	11.7	10.0	9.2	7.4	–	11.7	1.87
Scales in E1 row	79	79	81	80	82	81	83	82	79	–	83	—
Scales in continuous lateral line	81	77	77	78	77	80	78	77	77	–	81	—
Dorsal-fin spines	15	12	15	15	15	14	15	15	12	–	15	—
Dorsal-fin rays	18	17	17	17	17	18	16	18	16	–	18	—
Anal-fin spines	3	3	3	3	3	3	3	3		3		—
Anal-fin rays	11	11	11	10	12	11	11	11	10	–	12	—
Pectoral-fin rays	13	15	16	14	16	14	14	14	13	–	16	—
Gill rakers on 1st gill arch	17	19	20	20	22	ND	15	ND	15	–	22	—
Sex	female	ND	ND	ND	ND	male	female	ND				

In adults (Figs. 3, 5), background coloration counter shaded; dorsum and sides above pelvic fin grayish to light brown; ventrum creamy white in most specimens, but dusky in reproductive male. Mature male also with distinct dark area below nuchal hump. Holotype, presumably immature female, with irregular pattern of small white spots approximating size of one scale; white spots moderately spaced along sides from anterior dark blotch to caudal peduncle and dorsal-fin base to horizontal through middle of pectoral-fin base.

Anterior and posterior dark blotches in lateral series typically distinct and ocellated in adults. Anterior dark blotch (K&F marking 1) generally larger and more rounded overall (except in one large mature male where it appears reduced and un-ocellated); situated more or less level with dark postorbital markings and usually entirely below anterior lateral line (pale ocellus on lateral line in one specimen). Secondary anterior blotch sometimes present below and separate from main anterior blotch; secondary blotch vertically elongated and sometimes ocellated, its appearance obscured beneath folded pectoral fin. Posterior dark blotch (K&F marking 3) highly irregular in shape, sometimes broken into multiple ocellated blotches with the anteriormost one tall, subtriangular (pointed dorsally) and trailing ones much smaller, rounded; posterior blotch(es) shifted dorsally to position entirely above posterior lateral line (but not reaching dorsal-fin base). Condition of central dark blotch (K&F marking 2) in lateral series highly variable: often absent, but sometimes small or vertically expanded, ocellated or not; horizontally aligned with anterior blotch. Vertical bars associated with anterior, central and posterior blotches, respectively, absent or faint in adults; vertical bars associated with interspaces absent or extremely faint. Dusky longitudinal blotch on dorsal sides (aside dorsal-fin base) absent or faint.

Postorbital stripe present, highly broken into irregular series of small dark spots and blotches that are often ocellated. Preorbital stripe absent; occipital bar generally absent except for a darkened area immediately below nuchal hump in one mature male.

Dorsal fin solid gray in mature male; other specimens with rows of pale rounded windows that are especially evident in rayed portion of fin. Anal fin uniformly dark gray. Caudal-fin coloration typical of other species of *Cichla*: ocellated caudal blotch distinct and shifted to ventral half of base of dorsal caudal-fin lobe; dusky pigment leaving rows of pale rounded windows in dorsal lobe; ventral lobe with faint markings or, in larger specimens, solid gray. Pectoral fin hyaline to slightly dusky. Pelvic fin gray dorsally (fading to white medially in one large male), dusky to white ventrally.

Color in life.—Individuals vary greatly in coloration depending on age/size, sex, reproductive state and ecological conditions. Eye with large black pupil surrounded by narrow pale ring followed by wide outer ring of red or orange. Background color on sides of head and body varies from gray-green to yellow- or bronze-green. Some adults have sides of body with evenly-spaced white spots that become more conspicuous posteriorly. Underside of head white with yellow-green to tangerine color on portions of gular region and branchiostegals. Underside of body white from abdomen to end of caudal peduncle. Dark markings in lateral series (anterior, central and posterior blotches) black; each one ocellated with bright white or yellow. Caudal blotch and postorbital spots similarly black with bright white to yellow ocellus.

Dorsal fin and dorsal lobe of caudal fin gray with blue or blue-green tint; rows of pale spots conspicuous in soft dorsal fin and dorsal lobe of caudal fin. Ventral lobe of caudal fin and anal fin similarly colored, dusky yellowish- to reddish-orange, sometimes with greenish iridescence. Pelvic fins yellowish-orange. Pectoral fins translucent with yellowish-orange tint.

Distribution and habitat.—*Cichla cataractae* is only known from the Essequibo River channel and its major left-bank (western) tributaries draining the Guiana Shield uplands such as the Cuyuní, Mazaruni, Burro Burro and Rupununi (Fig. 7). The species is strongly associated with rocky shoals in flowing channels of clear to mildly turbid rivers. This affinity for water flowing over rocks is the reason for its local name, Falls Lukunani. Adults and subadults are not normally found in floodplain habitats, but the species likely enters flooded marginal areas during some periods and life stages (e.g., as brood-guarding adults or juveniles seeking food and refuge from predation).

Ecology.—Although we have no data on its diet and feeding, *Cichla cataractae* undoubtedly feeds primarily or exclusively on fish, like its congeners (Lowe-McConnell, 1969; Jepsen et al., 1997; Winemiller et al., 1997; Montaña et al., 2011; Marto et al., 2015). Fry are presumed to feed on zooplankton and other small aquatic invertebrates before shifting to a piscivorous diet. *Cichla cataractae* apparently grow larger than *C. ocellaris*. According to Mr. Ashley Holland, a local fishing guide from the Yupukari village, Falls Lukunani (*C. cataractae*) weigh up to 8 kg, with fish weighing 3–3.5 kg commonly caught. In contrast, the largest Pond Lukunani (*C. ocellaris*) he had seen weighed only 4.5 kg; but he received reports of fish weighing 5.5 kg. Anglers in Guyana commonly catch Pond Lukunani weighing 1–2.5 kg.

Cichla cataractae appears to be less abundant than *C. ocellaris* in rivers where the two co-occur. However, adult *C. cataractae* seem to be most common when fishing around rocky shoals in appropriate river reaches, whereas a few *C. ocellaris* may be caught near the shoreline or from habitats well sheltered from water current. Given its habitat affinity, *C. cataractae* is presumed to nest on rocky shoals in the river channel during seasons of low discharge in a manner similar to that observed for *C. intermedia* in Venezuela (KOW, pers. obs.). Male *C. cataractae* develop a bright red iris and nuchal hump prior to breeding, but the hump tends to be small in comparison to other species of *Cichla*.

Etymology.—Species name derived from *cataractae*, Latin for waterfall or rapids; treated as a noun in apposition.

Local names.—In Guyana, *Cichla cataractae* is often distinguished as the Falls Lukunani whereas *C. ocellaris* is considered the Pond Lukunani.

DISCUSSION

Under the aegis of the phylogenetic species concept, patterns of character distributions provide testable evidence for the existence of an elemental unit of nature – the species (Wheeler, 1999). In their comprehensive revision of *Cichla*, Kullander and Ferreira (2006) used patterns of external morphological characters, especially coloration, to resolve the genus into 15 phylogenetic species. More recent studies (Willis et al., 2010; 2012; 2013; 2015; Willis, 2017) examined patterns of molecular characters to test whether those species are informative with respect to the evolution of *Cichla* diversity. Those molecular studies upheld some of the species and relationships proposed on the basis of morphology, but also demonstrated a much more complex pattern suggestive of extensive hybridization and introgression across lineages. In both the morphological and molecular studies, interpretations of character distribution patterns were complemented by biogeographical and ecological data.

For example, Kullander and Ferreira (2006) provided morphological support for a clade composed of *C. kelberi*, *C. monoculus*, *C. nigromaculata, C. ocellaris* and *C. pleiozona*, species common to lentic habitats in lowland regions of the Amazonas Basin and Guianas. Willis et al. (2012; 2013) found strong molecular support for the same clade, but not for the monophyly of its constituent species. Instead, Willis et al. (2012; 2013) interpreted those five nominal species as evolutionary significant units that exchange genes over time within a more inclusive taxon (*C. ocellaris sensu lato*). In both the morphological and molecular analyses, the sister group to the *C. ocellaris* clade involved *C. orinocensis*, a species common to lowland regions of the Orinoco and Negro basins. Molecular analysis grouped *C. orinocensis* with *C. intermedia* and revealed that mitochondrial lineages within *C. orinocensis* nest within the *C. ocellaris* clade, evidence of both recent and ancient hybridization between the two groups (Willis, 2017).

Kullander and Ferreira (2006) also proposed a clade composed of *C. jariina*, *C. pinima*, *C. temensis*, *C. thyrorus* and *C. vazzoleri* that was diagnosed by two putatively unique aspects of color pattern: presence of light spots along the sides in regular rows and presence of ocellated vertical bars. Willis et al. (2012; 2013) expanded that clade to include *C. melaniae*, *C. mirianae* and *C. piquiti*. Once again, the molecular data failed to support the monophyly of species within the expanded clade, with the notable exception of *C. temensis*. A follow-up molecular study (Willis, 2017) firmly expanded *C. pinima* to include nominal species *C. jariina*, *C. vazzoleri* and *C. thyrorus* (i.e., *Cichla pinima sensu lato*), but noted this group as paraphyletic with some members more closely related to *C. melaniae*, *C. mirianae* and *C. piquiti*.

Fig. 7. Distribution of *Cichla cataractae*, n. sp., in the Essequibo Basin. Star denotes type locality. Base map by J. Armbruster.

Molecular analyses failed to support the strict monophyly of many species delimited by Kullander and Ferreira (2006), but did support a deep phylogenetic split in *Cichla* into two distinct groups, Clade A and Clade B (Willis et al., 2012; 2013). Clade A was composed of five species: *Cichla melaniae*, *C. mirianae*, *C. pinima* (including synonyms *C. jariina*, *C. thyrorus*, and *C. vazzoleri*), *C. piquiti* and *C. temensis*. Clade B was composed of three species: *C. orinocensis*, *C. intermedia*, and *C. ocellaris* (including synonyms *C. monoculus*, *C. nigromaculata*, *C. kelberi*, and *C. pleiozona*). Although most species of *Cichla* commonly occupy lentic habitats in rivers and lakes, a few prefer lotic habits associated with rocky river rapids, notably *C. intermedia*, *C. melaniae* and some populations of *C. pinima* (e.g., Jari Basin) (Jepsen et al., 1997; Winemiller et al., 1997; Winemiller, 2001; Stawikowski and Werner, 2004; Kullander and Ferreira, 2006).

Based on the molecular analyses reported here (Fig. 2), *Cichla cataractae* represents a distinct lineage of Clade-A *Cichla*. Another major lineage is represented by *C. temensis*, a species widely distributed in the Orinoco and north-central Amazonas basins, the latter including the Negro and Amazonas tributaries proximal to the mouth of the Negro (Kullander and Ferreira, 2006; Willis et al., 2015; Willis, 2017). Other species of Clade-A *Cichla* (*C. melaniae*, *C. mirianae*, *C. piquiti*, and *C. pinima* including synonyms *C. vazzoleri*, *C. thyrorus*, and *C. jariina*) showed a greater affinity in this topology; those species are all native to the lower Amazonas Basin and common to tributaries draining both the Guiana and Brazilian Shields (Kullander and Ferreira 2006; Willis, 2017). However, support for those and other relationships within Clade A was weak. As discussed by Willis (2017), relationships within clade A appear to be subject to incomplete lineage sorting and introgression, and resolution depends on the applied species concept. Like Clade-A members *C. melaniae* and some *C. pinima*, *C. cataractae* inhabits rocky river rapids, as does the Clade-B lineage represented by *C. intermedia*. The long molecular branch length for *C. cataractae* suggests that this species has long been isolated from other Clade-A members. The relationship between *C. cataractae* and its syntopic congener *C. ocellaris* is even more distant as it lies in the common ancestor of all extant *Cichla*.

COMPARATIVE MATERIAL

Cichla ocellaris.—Guyana: ANSP 39828 (2, 83.8-144.8 mm SL), Rupununi River, J. Ogilvie, 1911–1912; ANSP 176028 (1), Essequibo River, extensive sandbar near Essequibo campsite, 4°45’41”N, 58°45’53”W, W.G. Saul et al., 25 Jan 1997; ANSP 176030 (1, 216 mm SL), CSBD F 319 (1), Essequibo River, at Essequibo campsite, cove in front of camp, 4°45’41”N, 58°45’53”W, W.G. Saul et al., 25 Jan 1997; ANSP 176031 (1, 20.2 mm SL), Essequibo River, ca. two hours downstream from Kurupukari field station, 4°47’44”N, 58°48’52”W, W.G. Saul et al., 20 Jan 1997; ANSP 176032 (7), CSBD F 318 (2), Essequibo River, sand bar some 50 minutes upstream from Kurupukari field station, 4°42’47”N, 58°42’40”W, W.G. Saul et al., 27 Jan 1997; ANSP 177094 (2, 51.6–217.0 mm SL), Essequibo River, Yurrie Creek approx. 2.0 km upstream from Paddle Rock campsite, 4°42’3”N, 58°42’44”W, C. Watson et al., 26 Nov 1997; ANSP 187127 (1, 215 mm SL), Essequibo River at Yukanopito Falls, 44.5 km SW of mouth of Kuyuwini River, 1°54’53”N, 58°31’14”W, M.H. Sabaj et al., 9 Nov 2003; YPM 7962 (1), Pirara River, 3°37’19.6”N 59°40’18.5”W, E.C. Migdalski, 31 Jan 1953.

ACKNOWLEDGEMENTS

Thanks to Jonathan Armbruster and Nathan Lujan for reviewing the manuscript and providing helpful suggestions for improvement. For curatorial assistance including loans of specimens and tissues, we thank Mariangeles Arce H. (ANSP), David Werneke (AUM), David Catania (CAS), Caleb McMahan, Susan Mochel and Kevin Swagel (FMNH), Mary Burridge and Margaret Zur (ROM), Andrew Williston (MCZ), Douglas Nelson and Randy Singer (UMMZ), and Gregory Watkins-Colwell (YPM). For help in the field we thank Devin Bloom, Carmen Montaña, Erling Holm, Mary Burridge, Sarah Steele, Thomas Morgan, Kimberly Foster, Sean Anderson, Lesley de Souza, Nathan Lujan, Elford Liverpool, Calvin Bernard, Frances Hauser, Viviana Astudillo-Clavijo, Karen Alofs, Priya Maharaj, Mark Ram, Patrick Williams, Aiesha Williams, Ashley Holland and son Shannon, the staff of WWF-Guyana and Caiman House Field Station, and Diana Fernandes of the Guyana Environmental Protection Agency. Fieldwork in Guyana and Suriname between 2009 and 2016 supported by ROM grants to HLF; 2018 expedition to Guyana, during which the holotype and paratypes were collected, supported by funds from the University of Michigan to HLF.

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