AMERICAN MUSEUM NOVITATES

Number 3831, 18 pp. April 21, 2015

Phylogenetics of *Teleogramma*, a riverine clade of African cichlid fishes, with a description of the deepwater molluskivore—*Teleogramma obamaorum*—from the lower reaches of the middle Congo River

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ABSTRACT

The lower Congo River and nearby habitats harbor numerous endemic lineages of cichlid fishes, including some with highly specialized morphologies. Based on morphological and molecular data, we herein describe a new species of *Teleogramma*, a member of the chromidotilapiine clade found on rocky outcrops in the lower reaches of the middle Congo River. The new species, *T. obamaorum*, is distinguished from congeners by numerous morphological and ecological attributes, including the lack of dorsoventral head and body depression, absence of sexual dichromatism, and features of laterosensory anatomy, pharyngeal and gut morphology, and dietary preference. Phylogenetic analyses of two nuclear and two mitochondrial loci using Bayesian and maximum-likelihood inference lend strong support for the taxonomic validity of *T. obamaorum* and provide preliminary estimates of species relationships within the genus. The discovery of a new, ecomorphologically distinctive cichlid species in the Congo River suggests that additional research focus on riverine clades has the potential to greatly contribute to our understanding of evolutionary dynamics in this hyperdiverse group of teleost fishes.

KEYWORDS: Afrotropics, riverine biodiversity, molecular systematics, taxonomy

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INTRODUCTION

Teleogramma is a small clade of rheophilic, rock-dwelling cichlids restricted to fast-flowing waters in the western Congo basin. Unlike members of most riverine cichlid lineages, which exhibit muted morphological innovation and share a rather generalized "riverine cichlid" gestalt, *Teleogramma* species have highly specialized anatomies. When first described by Boulenger (1899), the genus was erroneously placed in the family Labridae. Myers (1939) and subsequent studies placed it within the Cichlidae, and all noted the highly distinctive nature of these unusual riverine cichlids. Takahashi and Nakaya (2001) provided a detailed anatomical description of *Teleogramma* and enumerated a suite of osteological and myological synapomorphies for the genus. Species within this genus are readily recognized by their markedly dorsoventrally compressed heads bearing a pair of prominent tubular nostrils, their elongate compressed bodies, and the presence of a single continuous lateral line not interrupted into upper and lower branches, as in most other cichlids.

Due in part to their highly autapomorphic morphology, determination of the interrelationships of *Teleogramma* within the Cichlidae has proven elusive in morphological analyses (e.g., Stiassny, 1997; Takahashi and Nakaya, 2001). However, a recent multilocus phylogeny (Schwarzer et al., 2014) provides conclusive support for the placement of *Teleogramma* as nested within the chromidotilapiine lineage of African cichlids. Chromidotilapiines are a primarily riverine clade that originated in West and Central Africa in the late Eocene/early Oligocene (Schwarzer et al., 2014), and therefore represent an early African cichlid radiation with origins long predating those of the hyperdiverse, predominately lacustrine, assemblages of eastern Africa.

Prior to the present study, *Teleogramma* was considered to contain four species (Roberts and Stewart, 1976), three of which are endemic to rocky outcrops in fast-flowing waters along stretches of the lower Congo River (LCR): *T. brichardi* (fig. 1A), *T. gracile* (fig. 1B), and *T. depressa* (fig. 1C). A fourth species, *T. monogramma* (fig. 1D), occurs in rapids-associated outcrops below the confluence of two Congo tributaries, the Lulua and Kasai, located some 850 river kilometers upstream from the outflow of the LCR from Pool Malebo.

During a period of exceptionally low water throughout western Congo in the summer of 2011, a series of highly distinctive specimens were collected in newly exposed rocky outcrops along the lower reaches of the middle Congo River just upstream of Pool Malebo (fig. 2). These specimens were unassignable to any previously described species. Preliminary morphological examination suggested that, although lacking a number of distinctive features of the genus described by Takahashi and Nakaya (2001), these specimens likely represented an undescribed species of *Teleogramma*, a finding fully corroborated in the present study with both morphological and molecular evidence.

In addition to detailed morphological examination, and in order to phylogenetically place the new species within the genus, representatives of all putative *Teleogramma* species and a chromidotilapiine outgroup were sequenced for two nuclear (SH3PX3 and Ptr) and two mitochondrial (CO1 and ND2) loci. Model-based phylogenetic reconstructions were undertaken on these molecular data and the results of those analyses provide a comparative framework for the formal taxonomic description of the distinctive new species, *Teleogramma obamaorum*, provided herein.

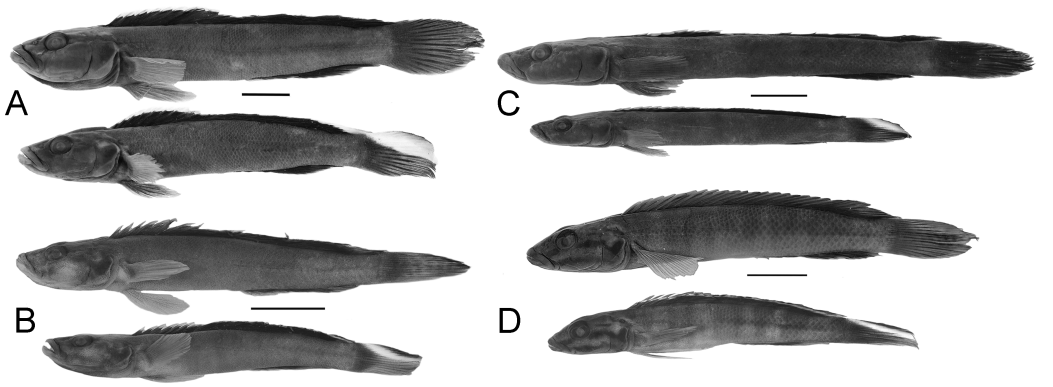

FIGURE 1. *Teleogramma* (Boulenger, 1899) general habitus of currently recognized species, in lateral aspect, ♂ above, ♀ below. **A,** *T. brichardi* (AMNH 246986); **B,** *T. gracile* (AMNH 247261); **C,** *T. depressa* (AMNH 239325); **D,** *T. monogramma* (AMNH 247806 ♂, 253127 ♀). Scale bars = 1 cm.

Materials and Methods

Morphology: Fourteen standard morphometric measurements and seven meristic counts were taken following Barel et al. (1977). Specimens were carefully pinned flat and photographed on the left side using a Nikon Digital SLR camera with a 60 mm f/2.8 AF Micro-Nikkor lens. Linear measurements were then taken using the open access software ImageJ v1.48 (Schneider et al., 2012), and vertebral and fin-ray counts were taken from radiographed and/or cleared and stained specimens. Gill raker counts are totals for the first arch and include the raker at the junction of ceratobranchial and epibranchial elements. Lateral-line counts exclude the small pored scales on the caudal fin distal to the point of caudal flexion. For comparative purposes, corresponding counts and measurements for the closely related *T. monogramma* and *T. brichardi* are provided. Additional specimens of all putative species were examined and cleared and stained using a modified protocol of Taylor and Van Dyke (1985).

Abbreviations used throughout the text are: **C&S,** cleared and stained preparations; **SL,** standard length; **HL,** head length; **ex,** number of specimens examined. Institutional abbreviations follow Sabaj Perez (2014).

Molecular Methods: Total genomic DNA was extracted from fin clips using the DNeasy tissue extraction kit (Qiagen). Partial sequence fragments of four genetic markers (two mitochondrial: cytochrome oxidase I (COI) and NADH dehydrogenase subunit 2 (ND2) (Kocher et al., 1995), and two nuclear: SH3PX3 and Ptr (Li et al., 2007)) were sequenced across representatives of all putative *Teleogramma* species. Based on the phylogenetic hypothesis of Schwarzer et al. (2014), the type species of the genus *Chromidotilapia* sensu stricto (*Chromidotilapia kingsleyae*) was selected as an outgroup for rooting the *Teleogramma* trees. DNA amplification via PCR was performed with illustra PuReTaq Ready-To-Go PCR Beads (GE Healthcare). For COI, we used primers VF2_t1, 5′-TGTAAAACGACGGCCAGTCAACCAACCACAAAGACATTGGCAC-3′, FishF2_t1, 5′-TGTAAAACGACGGCCAGTCGACTAATCATAAAGATATCGGCAC-3′,

FishR2_t1, 5′-CAGGAAACAGCTATGACACTTCAGGGTGACCGAAGAATCAGAA-3′, and FR1d_t1, 5′-CAGGAAACAGCTATGACACCTCAGGGTGTCCGAARAAYCARAA-3′ (Ivanova et al., 2007) with the following amplification conditions: 94° C for 2 min, 35 cycles of 94° C for 30 s, 52° C for 40 s, and 72° C for 1 min, with a final extension at 72° C for 10 min. For the ND2 marker, we used primers ND2Trp, 5′-CATACCCCAAACATGTTGGT-3′ and ND2Met, 5′-GTSGSTTTTCACTCCCGCTTA-3′ (Kocher et al., 1995) with the following amplification conditions: 94° C for 2 min, 35 cycles of 94° C for 30 s, 55° C for 30 s, and 72° C for 1 min, with a final extension at 72° C for 10 min. For nuclear markers, amplifications were performed using primers Ptr_F458, 5′-AGAATGGATWACCAACACYTACG-3′ and Ptr_R1248, 5′-TAAGGCACAGGATTGAGATGCT-3′, and SH3PX3_F461 (5′-GTATGGTSGGCAGGAACYTGAA-3′) and SH3PX3_R982 (5′-CAAACAKCTCYCCGATGTTCTC-3′) (Li et al., 2007), with the following amplification conditions for both: 94° C for 2 min, 35 cycles of 94° C for 30 s, 55° C for 40 s, and 72° C for 1 min, with a final extension at 72° C for 10 min. Successful amplifications were sequenced at Genewiz Inc. (South Plainfield, NJ).

Forward and reverse chromatograms were edited and aligned using Geneious R7.0 (Biomatters Ltd., Aukland, NZ). Alignment across all specimens was performed using MUSCLE v3.5 (Edgar, 2004), and best-fit models of nucleotide evolution were determined using JModeltest (Evolutionary Biology Centre, Uppsala University, Sweden). To accommodate heterogeneity between gene regions, model-based analyses were conducted on the concatenated alignment partitioned into gene regions with parameters unlinked. Likelihood analyses were carried out in RAxML v7.2.8 Black Box (Stamatakis, 2006), and Bayesian phylogenetic inference using Markov Chain Monte Carlo (MCMC) methods was implemented in MrBayes v3.2 (Huelsenbeck and Ronquist, 2001). Runs were performed using 15 million generations with trees sampled every 1000 generations, and a burn-in of 25%. In the likelihood analyses nodal support is given by means of bootstrap character resampling (1000 pseudoreplicates), and Bayesian nodal support was assessed using Markov chain Monte Carlo sampling to derive posterior probabilities. Specimen voucher data and GenBank accession numbers for all loci generated in the current study are provided in table 1.

RESULTS

Phylogenetic Analyses

Likelihood and Bayesian model-based phylogenetic analyses resulted in the same topology (fig. 3), and provide strong support for the generic placement and taxonomic validity of *Teleogramma obamaorum*. The results of this small-scale analysis also provide a preliminary estimate of species relationships with the genus, which is partitioned into two main clades. Within "clade A" the new species, *T. obamaorum*, is resolved as sister to the Kasai/Lulua–dwelling *T. monogramma,* and together these are sister to *T. brichardi*. We note that *T. brichardi,* as recognized herein, is restricted to specimens from the immediate vicinity of the type locality at the fishing village of Kinsuka, located on the left bank of the LCR at the first rapids downstream of Pool Malebo in the Democratic Republic of Congo (fig. 2).

TABLE 1. Taxa, voucher catalog numbers, and GenBank accession numbers for the gene sequences included in the analyses.

Taxon	AMNH catalog	Tissue code	GenBank Accession Number			
			nd2	*co1*	*ptr*	*sh3px3*
OUTGROUP						
Chromidotilapia kingsleyae	AMNH 263142	227313	KP714163	KP714158	KP714196	KP714215
INGROUP						
Teleogramma obamaorum, n. sp.	AMNH 255206	224324	KP714162	n/a	KP714191	KP714213
Teleogramma obamaorum, n. sp.	AMNH 255329	223886	KP714165	KP714156	KP714194	KP714212
Teleogramma obamaorum, n. sp.	AMNH 255329	223885	KP714170	KP714155	KP714193	KP714211
Teleogramma obamaorum, n. sp.	AMNH 255329	223881	KP714177	n/a	KP714192	KP714210
Teleogramma monogramma	AMNH 247831	055-5455	KP714174	KP714149	KP714184	KP714204
Teleogramma monogramma	AMNH 247780	055-5483	KP714159	KP714151	KP714186	KP714206
Teleogramma monogramma	AMNH 247780	055-5482	KP714169	KP714150	KP714185	KP714205
Teleogramma monogramma	AMNH 247819	061-6024	KP714160	KP714152	KP714188	KP714207
Teleogramma brichardi	AMNH 246986	061-6026	KP714176	KP714154	KP714190	KP714209
Teleogramma brichardi	AMNH 240012	024-2338	KP714167	KP714143	KP714178	KP714197
Teleogramma brichardi	AMNH 246986	061-6025	KP714161	KP714153	KP714189	KP714208
Teleogramma depressa	AMNH 240013	035-3425	KP714168	KP714145	KP714180	KP714199
Teleogramma depressa	AMNH 240013	035-3426	KP714164	KP714146	KP714181	KP714200
Teleogramma depressa	AMNH 255381	224163	KP714171	KP714157	KP714195	KP714214
Teleogramma depressa	AMNH 239324	060-5942	HM101360	n/a	n/a	n/a
Teleogramma depressa	AMNH 239324	060-5945	KP714175	KP714141	KP714187	KP714203
Teleogramma depressa	AMNH 239324	060-5943	HM101359	n/a	n/a	n/a
Teleogramma depressa	AMNH 241068	033-3212	KP714172	KP714144	KP714179	KP714198
Teleogramma gracile	AMNH 246477	043-4296	KP714166	KP714147	KP714182	KP714201
Teleogramma gracile	AMNH 246477	043-4297	KP714173	KP714148	KP714183	KP714202

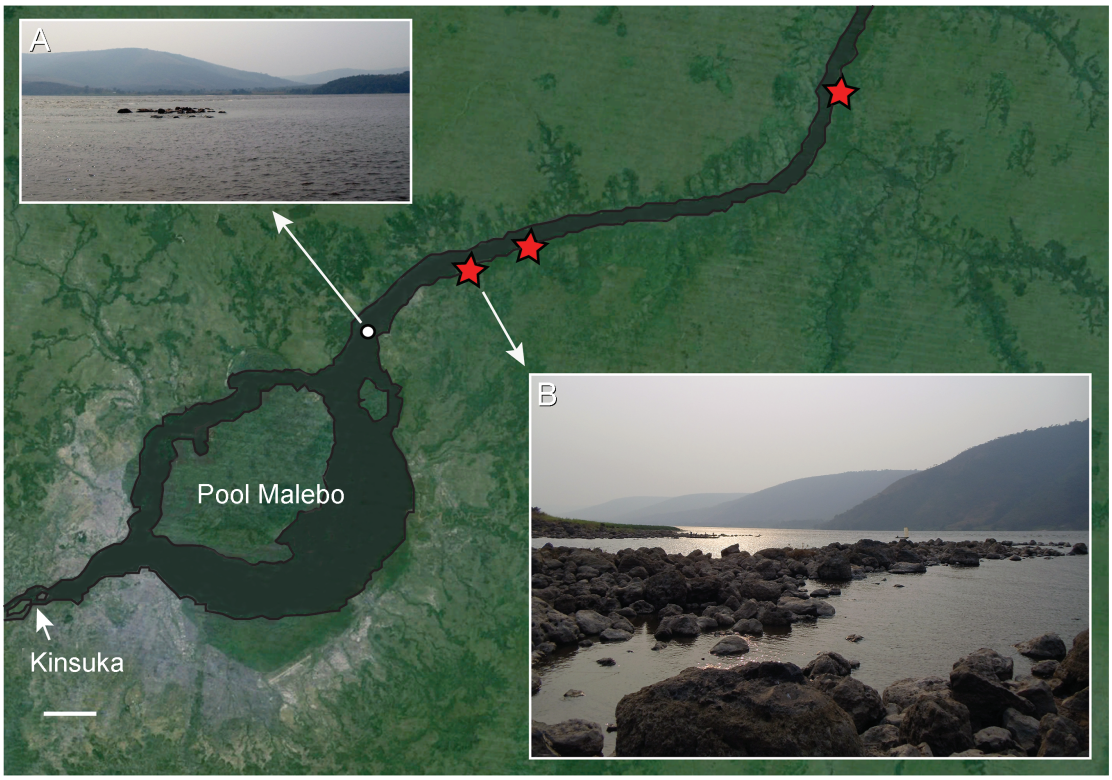

FIGURE 2. Collection sites of *T. obamaorum*, new species (red stars) along lower reach of middle Congo above Pool Malebo. **A,** exposed rocks in midstream of Congo River main channel just above Pool Malebo; **B,** collection site of holotype, among exposed rocks extending into main channel. Inset photographs taken in August 2011 at a time of record low water throughout western Congo.

While support is strong for the monophyly of "clade B" *Teleogramma*, which comprises the remainder of the LCR populations, branch lengths in this region of the tree are extremely short and the resultant topology highlights conflict between morphology-based taxonomy versus molecular signal. Such short branch lengths, in conjunction with molecular and morphological discord, suggest that rapid and recent divergence, and perhaps ongoing gene flow between incipient and/or young species, may be confounding the molecular signal provided by the four molecular markers used in this study. To further investigate the population dynamics, relationships, taxonomic status, and age of the LCR *Teleogramma* we are currently analyzing a genomewide sampling of *Teleogramma* populations utilizing restriction site associated (ddRAD) markers (Alter et al., in prep.). Despite the inability of our four-locus dataset to entirely resolve the species composition and relationships among the LCR "clade B" *Teleogramma*, in contrast "clade A" taxa are well supported by these data. Based on our molecular analyses, and a series of morphological and ecological attributes discussed below, we provide a formal taxonomic description of a new species of *Teleogramma, T. obamaorum,* a taxon geographically located between the widely disjunct LCR and Kasai/Lulua populations.

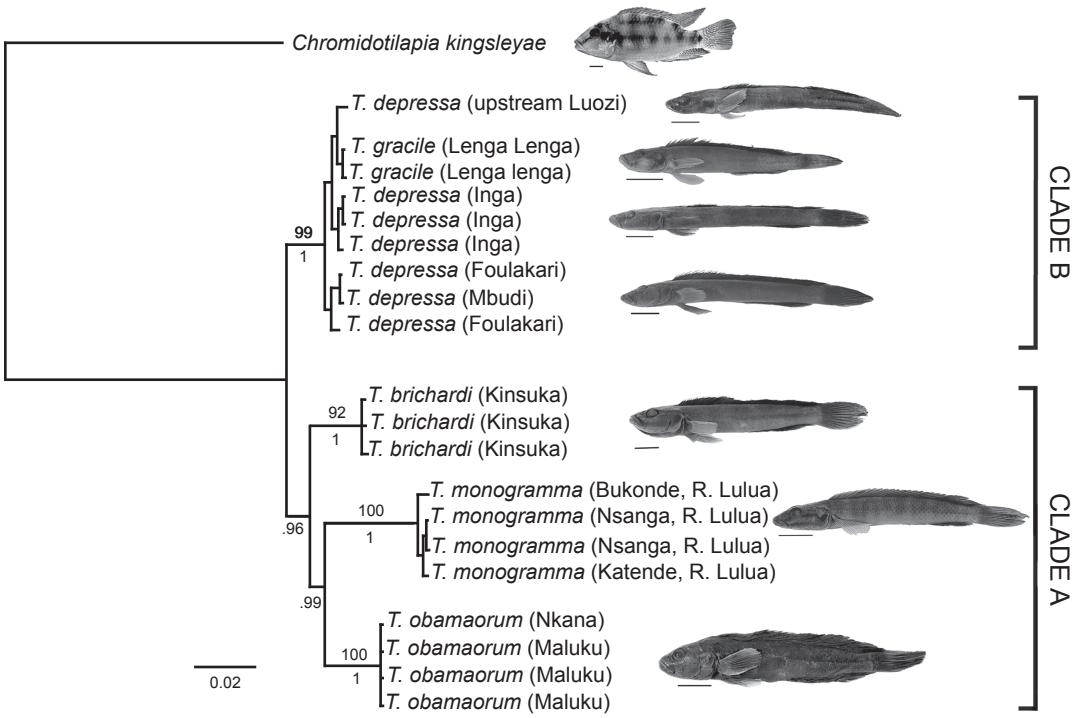

FIGURE 3. Maximum-likelihood phylogeny of *Teleogramma* (Baysian analysis resulted in an identical topology). Bootstrap support (>90%) indicated above internal nodes and posterior probabilities (>0.90) below. Collection localities of sampled individuals indicated in parentheses.

Teleogramma obamaorum, new species

Figures 4–8, tables 2 and 3

Holotype: AMNH 264012, male, 75.00 mm SL, Democratic Republic of Congo, Kinshasa Province, main channel of middle Congo River at rocky outcrop en route to Mayi Ndombe River (4° 01′ 31.4″S, 15° 36′ 37.1″E), M.L.J. Stiassny et al., 10 August 2011.

Paratypes: AMNH 254857, 6 paratypes, 44.6–63.4 mm SL, same locality as holotype. — MRAC B5-04-P-1, 1 paratype, 59.4 mm SL, same locality as holotype. — AMNH 255206, 6 paratypes, 52.1–68.2 mm SL, Democratic Republic of Congo, Kinshasa Province, main channel of middle Congo River at rocky outcrop above guard post at Nkana (3° 53′ 31.4″S, 15° 55′ 27.9″E), M.L.J. Stiassny et al., 14 August 2011. — MCZ 171655, 1 paratype, 63.0 mm SL, Democratic Republic of Congo, Kinshasa Province, main channel of middle Congo River at rocky outcrop above guard post at Nkana (3° 53′ 31.4″S, 15° 55′ 27.9″E), M.L.J. Stiassny et al., 14 August 2011. — AMNH 255329, 4 paratypes, 48.8–64.9 mm SL, Democratic Republic of Congo, Kinshasa Province, main channel of middle Congo River at rocky outcrop above Maluku (4° 00′ 48.6″S, 15° 38′ 42.8″E), M.L.J. Stiassny et al., 14 August 2011. —ZSM 43801, 1 paratype, 58.9 mm SL, Democratic Republic of Congo, Kinshasa Province, main channel of middle Congo River at rocky outcrop above Maluku (4° 00′ 48.6″S, 15° 38′ 42.8″E), M.L.J. Stiassny et al., 14 August 2011.

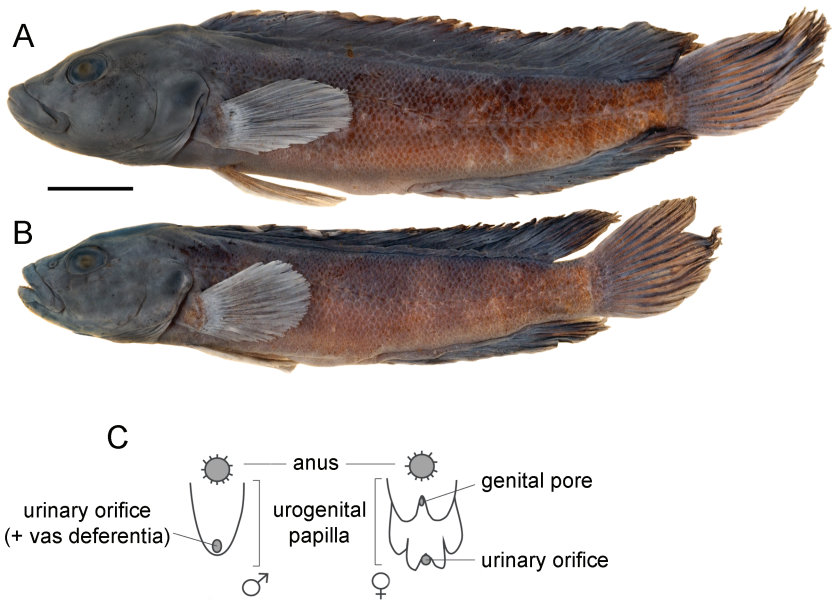

FIGURE 4. *T. obamaorum*, new species, general habitus, lateral view, in preservation. **A,** ♂ holotype (AMNH 264012); **B,** ♀ paratype (AMNH 254857); **C,** schematic representation of genital papillae. Scale bar = 1 cm.

Additional Nontype Material Examined: AMNH 264013, 3 specimens, Democratic Republic of Congo, Kinshasa Province, main channel of middle Congo River at rocky outcrop en route to Mayi Ndombe River (4° 01′ 31.4″S, 15° 36′ 37.1″E), M.L.J. Stiassny et al., 10 August 2011. — AMNH 264014, 3 specimens, Democratic Republic of Congo, Kinshasa Province, main channel of middle Congo River at rocky outcrop above guard post at Nkana (3° 53′ 31.4″S, 15° 55′ 27.9″E), M.L.J. Stiassny et al., 14 August 2011. — AMNH 264015, 3 specimens, 2 C&S, Democratic Republic of Congo, Kinshasa Province, main channel of middle Congo River at rocky outcrop above Maluku (4° 00′ 48.6″S, 15° 38′ 42.8″E), M.L.J. Stiassny et al., 14 August 2011.

Diagnosis: *Teleogramma obamaorum* is distinguished from all congeners by the absence of a sexual dichromatism of the caudal fin (versus caudal fin of females with a distinctively marked dorsal blaze), markedly inflated pores in the laterosensory system of the head, jaws, suspensorium and infraorbital series. It has 5 separate infraorbital elements (versus 4 in congeners), and a robust lower pharyngeal jaw (versus a markedly more gracile element in congeners). Uniquely among congeners, *T. obamaorum* is a robust species lacking dorsoventral head and body depression. It is further readily distinguished from *T. monogramma* by number of anal spines (7–8 versus 4), and from *T. brichardi* in the possession of 32–35 pored lateral-line scales (versus 51–60).

Description: A *Teleogramma* species attaining maximum-recorded size of 75.0 mm SL (mature male holotype, AMNH 264012), with general body shape and appearance in figure 4. Proportional measurements for holotype and 19 paratypes, and comparable ranges for *T. monogramma* and *T. brichardi*, the taxa that molecular analysis suggests most closely related (fig. 3),

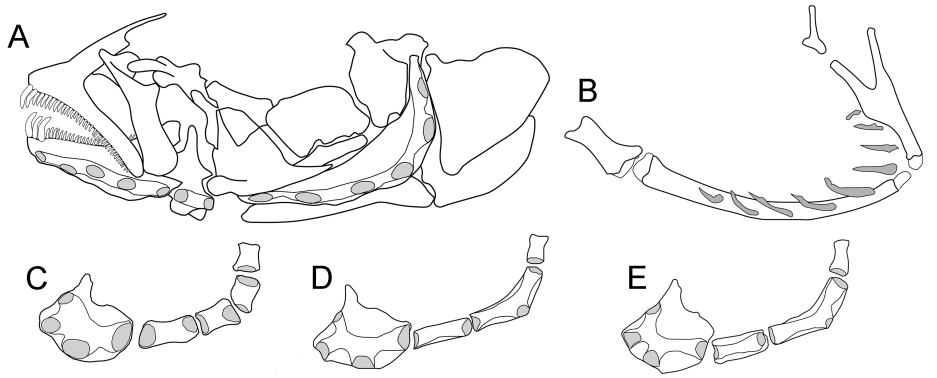

FIGURE 5. *T. obamaorum*, new species. **A,** oral jaws and suspensorium; **B,** first gill arch; **C,** infraorbital series; **D,** *T. monogramma*, infraorbital series; **E,** *T. brichardi*, infraorbital series.

are given in table 2 and meristic attributes summarized in table 3. Body deep and laterally compressed, with greatest depth at level of first dorsal fin spine. Dorsal and ventral body profiles slightly convex to relatively short, deep, caudal peduncle. Head robust rather than dorsoventrally compressed. Adductor mandibulae muscle complex markedly enlarged lending bulging appearance to the cheeks. Snout prominent and bears single, tubular, nostril on either side. Snout and dorsal head profile rise at angle of 35°–40° to midorbit, often with small, fat-filled, nuchal hump just anterior to dorsal fin origin in both sexes.

Dorsal fin XXI–XXIII (mode: XXII) 8 or 9 (mode: 9). Anal fin VII–VIII (mode: VII) 8–9 (mode 9); both with prominent, scaleless, fleshy bases. Dorsal-fin spines gradually increase in length posteriorly to around 8th spine then coequal in length. Posteriormost branched fin rays of dorsal and anal fins reach to anterior third of caudal fin. Caudal fin large and paddle shaped, with 14-branched rays (7+7) and rounded symmetrical distal margin. Pectoral fins broadly fan shaped, long but falling short of anus, with 15–16 rays. Pelvic fins falling just short of anus, with third branched ray longest in both sexes.

Jaws prominent, slightly prognathous and robust with lips well developed and fleshy. Inner and outer row teeth of both jaws pointed unicuspid. Single series of 2–3 enlarged, recurved canines situated anteriorly on premaxilla. Dentary with 3 enlarged canines anteriorly, larger pair slightly displaced dorsolaterally. Remaining outer row of teeth in both jaws gradually taper in size and extend almost entire length of both jaws (fig. 5A). Four or 5 inner rows of small, slightly recurved, unicuspid teeth clustered on anterior third of dentary; no inner rows distally on lower jaw. Two or three inner tooth rows anteriorly on premaxilla, tapering to single row terminating at two-thirds of length of dentigerous arm. Lower pharyngeal jaw is markedly more robust than in congeners with slightly sinuous, rather than straight, ventral suture (compare e.g., figs. 6A and B, C). Usually 15–16 moderately robust, unicuspid teeth in posterior row. Symphysial teeth enlarged and somewhat molariform (fig. 6A). Gill rakers elongate, nondenticulate and slender (fig. 5B). Eight to 10 rakers along outer row of first gill arch; 5–6 ceratobranchial rakers, usually one raker in angle of arch, and 2 or 3 epibranchial rakers.

TABLE 2. Morphometric data for type series of *Teleogramma obamaorum*, new species with comparative ranges for *T. monogramma* and *T. brichardi*.

	Teleogramma obama new species					*T. monogramma* (*n* =20)			*T. brichardi* (*n* =20)		
	Holtype	***N***	**Mean**	**Range**	**SD**	**Mean**	**Range**	**SD**	**Mean**	**Range**	**SD**
Standard Length (mm)	75.0			44.6–75.0		60.6	49.9–75.4		84.3	47.8–87.7	
% Standard length											
Body depth	21.8	20	20.3	18.4–21.8	0.88	14.7	12.0–16.7	1.47	16.8	15.1–19.9	1.24
Head length	27.5	20	29.0	25.8–31.2	1.51	26.6	23.3–28.0	1.27	28.5	25.0–30.3	1.27
Predorsal length	29.5	20	30.2	27.6–32.3	1.30	27.2	25.9–29.1	0.94	27.4	26.1–28.8	0.88
Preanal length	60.8	20	60.6	57.6–64.2	1.90	61.0	59.6–63.8	1.10	61.4	59.1–63.5	1.23
Caudal peduncle depth	10.5	20	10.3	9.5–11.2	0.38	9.2	85.–10.0	0.46	10.4	9.2–11.4	0.62
Caudal peduncle length	14.8	20	14.2	12.0–16.1	1.01	17.9	15.8–19.9	1.07	16.3	14.6–17.4	0.90
Anal-fin base length	29.6	20	28.1	24.7–31.6	1.72	23.0	20.6–25.7	1.28	23.9	21.2–26.8	1.58
Dorsal-fin base length	64.5	20	64.1	60.2–66.5	1.85	64.7	61.3–67.4	1.77	66.7	64.2–68.9	1.12
% Head Length											
Lower-jaw length	55.3	20	45.3	39.4–55.3	4.45	46.9	42.7–57.3	3.31	45.1	41.3–53.0	3.78
Upper-jaw length	38.3	20	35.7	31.4–39.5	2.27	36.3	32.4–39.1	1.68	30.0	26.5–33.6	1.87
Eye diameter	21.2	20	21.7	19.6–24.2	1.50	21.9	19.2–26.4	1.73	21.6	20.0–24.0	1.02
Snout length	29.0	20	29.9	26.0–34.5	2.20	28.1	23.1–34.0	2.56	30.0	26.5–33.6	1.87
Interorbital width	15.0	20	14.5	10.7–19.6	2.37	14.8	13.2–17.9	1.43	16.1	12.0–21.8	2.85

TABLE 3. Meristic data for type series of *Teleogramma obamaorum*, new species with comparative ranges for *T. monogramma* and *T. brichardi*.

(*modal count)	*T. obama* (*n* = 20)	*T. monogramma* (*n* = 20)	*T. brichardi* (*n* = 20)
Lateral-line scales	32–35 (*34)	31–36 (*35)	51–60 (*55)
Dorsal-fin spines and rays	XXI 9-XXIII 8 (*XXII 9)	XIX–XX 10–11 (*XX 11)	XXII–XXIV 6–8 (*XXIII 7)
Anal-fin spines and rays	VII 8-VIII 9 (*VII 9)	IV 9–11 (*IV 10)	IV-VI 8–10 (*V 9)
Gill rakers	5,1,2–6,1,3 (*6,1,3)	3,1,1–4,1,2 (*3,1,2)	3,1,1–5,1,2 (*5,1,2)
Total number of vertebrae	30–32 (*32)	32–33 (*33)	31–32 (*32)
Precaudal vertebrae	13–14 (*13)	13–14 (*13)	13–14 (*13)
Caudal vertebrae	17–20 (*19)	19–20 (*20)	18–19 (*19)

All scales cycloid, with those on flanks small and somewhat irregularly sized. Entire head and nape proximal to dorsal-fin origin naked. Pectoral base and chest naked, scales over ventrum to anus very small and deeply embedded. Scales immediately below dorsal-fin fold to level of 10–12th dorsal-fin spine markedly smaller than those on flanks. Proximal third of caudal fin covered with small ovoid, scales. Lateral line continuous and undivided; comprised of 32–35 elongate, pored scales, each approximately twice as large as unpored scales of upper and lower flanking rows. Often 1 or 2 pored scales embedded distal to line of caudal flexion on caudal base. Total number of vertebrae: 30–32, comprised of 13–14 precaudal and 17–20 abdominal centra.

Supraoccipital crest extremely low, with no frontal ridge extending to neurocranial lateral-line foramen. All neurocranial, dental and preopercular sensory canals inflated with foramina greatly enlarged (fig. 5A). Infraorbital series (fig. 5C) consisting of square, platelike first infraorbital (lachrymal) bearing 4 inflated, sensory-canal pores. Second, third, fourth, and fifth (dermosphenotic) infraorbital elements separate, each with inflated sensory canal and enlarged pores. All congeners with infraorbital elements 3 and 4 fused, without sensory-canal pores markedly inflated (e.g., figs. 5D,E). No supraneural between neurocranium and first dorsal-fin pterygiophore.

GUT MORPHOLOGY AND DIET: Digestive tract short, total length (unraveled but not stretched) ca. 60%–65% SL. Esophagus leads to small bulbous stomach, from which intestine exits left side at transition zone between esophagus and stomach. Proximal descending limb of intestine wide anterior to rostrocaudad loop. Distal limb descending to anus also extremely wide (fig. 7A). All congeners (e.g., figs. 7B,C) with proximal descending limb of intestine wide—a feature interpreted here as a putative synapomorphy of the genus—whereas distal limb is narrow and similar to condition in other cichlids (Zihler, 1982; Tougas and Stiassny, 2014). Stomach and full length of gut of all specimens contained small, intact shells of two species of rissooidean gastropods (superfamily Rissooidea) (fig. 8). In most cases no other food items were present, although few individuals also contained some disarticulated remains of ephemeropteran nymphs.

REPRODUCTION: Unlike congeners, male and female *T. obamaorum* are monomorphic, distinguished externally only by examination of the genital papilla (fig. 4C). The contrasting caudal-fin coloration and patterning characteristic of females of other *Teleogramma* species (e.g., fig. 1) is lacking and caudal fins of both females and males are uniformly colored with no

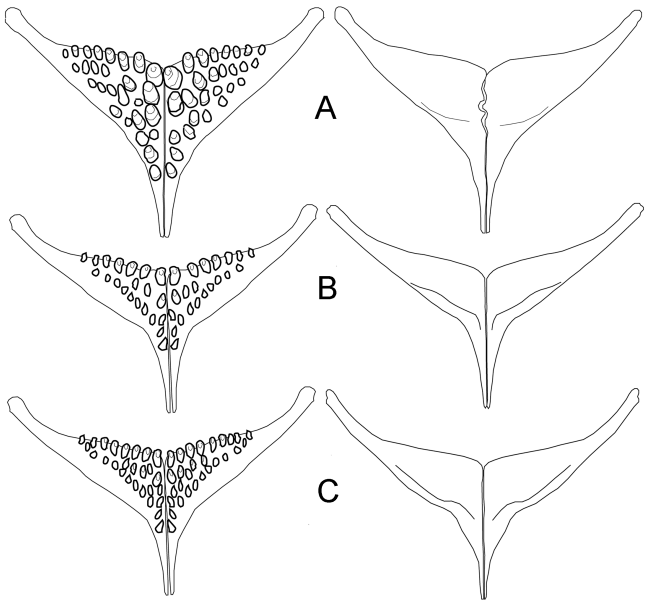

FIGURE 6. Isolated lower pharyngeal jaw (fifth ceratobranchial elements), in dorsal (left) and ventral (right) views. **A,** *T. obamaorum*; **B,** *T. monogramma*; **C,** *T. brichardi*.

dorsal blaze of contrasting color or pigmentation. Males and females are similarly colored in life with base body coloration uniform smoky, grayish black becoming pale yellowish gray ventrally. Although collected while reproductively active, female *T. obamaorum* also appear to lack the pronounced red flush of color on the belly that characterizes females of other *Teleogramma* species (Roberts and Stewart, 1976) and most chromidotilapiines (Lamboj, 2004). In preservation (fig. 4), the base body coloration is dark brownish black, slightly darker dorsally becoming paler ventrally. Unpaired fins are uniformly blackish brown.

Fecundity appears to be low. The largest female of *Teleogramma obamaorum* examined (63.8 mm SL) contained only 19 ovoid eggs measuring approximately 2 mm in height and 1.8 mm at widest girth and the smallest female (51.9 mm SL) contained 15 eggs of a similar size. In contrast, egg numbers in ripe individuals of similar sized *T. brichardi* and *T. monogramma* were higher, averaging 25 to 35. Although some *T. obamaorum* specimens were "spent," most females contained ripening or fully mature eggs in paired ovaries and in most males' testis development was advanced, indicating that our collections were made during a reproductive period for the species.

Distribution and Habitat: Currently *Teleogramma obamaorum* is known only from a few rock outcrops located along a 40 km stretch of the middle Congo River, just upstream of Pool Malebo, in the Democratic Republic of Congo (fig. 2). All specimens were collected during August 2011. Water levels in the main channel of the middle Congo reached an historic low during this period (July–September 2011) which forced the cessation of commercial transportation as the river became nonnavigable to all but small shallow-draft pirogues (e.g., fig.

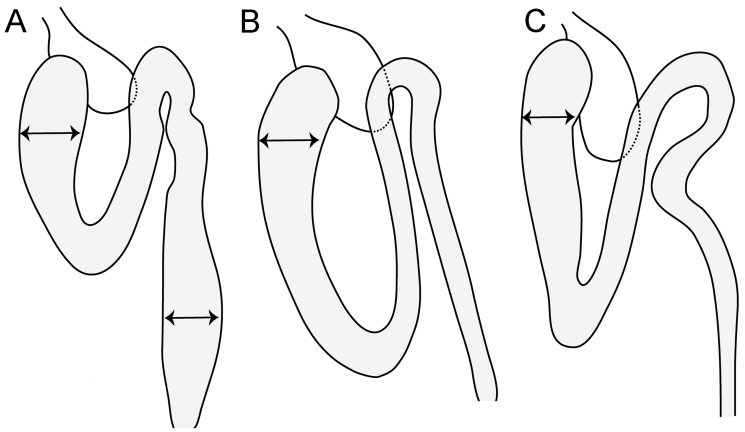

FIGURE 7. Digestive tracts (slightly unraveled for clearer depiction of morphology), after removal of liver, pancreas, gallbladder, spleen and adherent tissues. **A,** *T. obamaorum*; **B,** *T. monogramma*; **C,** *T. brichardi*. Double-headed arrows indicate regions of intestinal widening.

2A). At this time a series of rocky outcrops, that in previous (and subsequent) years had been completely submerged, were partially exposed and accessible for sampling and it was only on these that specimens of *T. obamaorum* were collected (e.g., fig. 2B). On the right bank of the Congo River in the Republic of Congo, and further upstream on the left bank in the Democratic Republic of Congo, very few rocky outcrops were located, and most of the shoreline was comprised of sandy or reed-fringed banks, suggesting that the short stretch where all *T. obamaorum* specimens were collected may represent the entire distributional range of the species.

Etymology: We name this new cichlid species from the freshwater heart of the African continent in honor of U.S. President Barack Obama and First Lady Michelle Obama, in recognition of their commitment to science education, development, gender equality, and self-reliance for all peoples of African nations, and their dedication to environmental conservation in Africa and beyond. Following recommendation 31.1.2. of the International Code of Zoological Nomenclature (1999) the specific name is treated as a noun in the genitive plural case.

Comparative Material Examined: *Teleogramma brichardi*: MCZ 48008, (ex. 8), 1 C&S, Democratic Republic of Congo, Congo River, rapids at Kinsuka near Kinshasa. — MCZ 48009, (ex. 4), 1 C&S, Democratic Republic of Congo, Congo River, rapids at Kinsuka near Kinshasa. — AMNH 240012, (ex. 5), 2 C&S, Democratic Republic of Congo, Congo River, Kinsuka, along margin of main channel, near but removed from large rapid. — AMNH 246985, (ex. 6), Democratic Republic of Congo, Kinsuka. — AMNH 250435, (ex. 2), Democratic Republic of Congo, Left bank Congo River, Kinsuka Rapids. — AMNH 263861, (ex. 1), Democratic Republic of Congo, Main channel of Congo River, Kinsuka Rapids.

Teleogramma depressa: MCZ 50559, paratypes, (ex. 5), 1 C&S, Democratic Republic of Congo, Congo River mainstream near Inga hydroelectric dam. — MCZ 50161, paratypes, (ex. 6), Democratic Republic of Congo, Congo River at Gombe or Ngombe, about 20 km W of Kinshasa, rapids in mainstream. — AMNH 239326, (ex. 5), Democratic Republic of Congo, main channel of Congo River, 2 km upstream of Kinganga. — AMNH 239324, (ex. 10), 2 C&S,

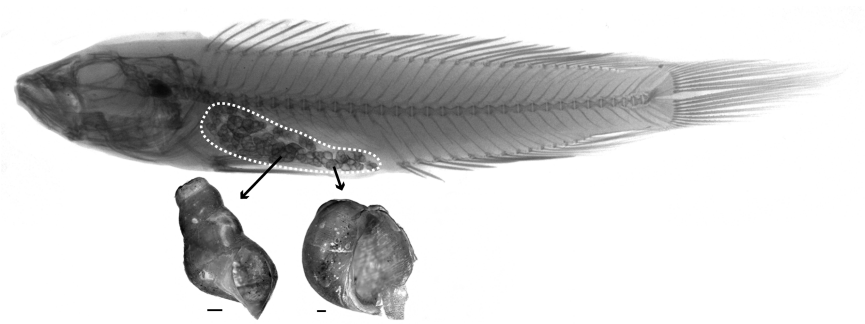

FIGURE 8. Radiograph, *T. obamaorum*, new species with close-up of two rissooidean gastropod shells extracted from the intestine. Scale bars = 0.1 mm.

Democratic Republic of Congo, main channel of Congo River, adjacent to Inga rapid, just below Inga intake canal. — AMNH 241068, (ex. 3), Democratic Republic of Congo, north bank of main channel of Congo River, upstream from Luozi — AMNH 240013, (ex. 6), 2 C&S, Republic of Congo, near camp at Foulakari, just off main channel of Congo River in rocks. — AMNH 239323, (ex. 5), 1 C&S, Republic of Congo, Congo River at start of rapids below Pool Malebo. — AMNH 255418, (ex. 3), Democratic Republic of Congo, main channel of lower Congo River at massive rocky outcrop at Ngombe. — AMNH 239321, (ex. 4), 1 C&S, Republic of Congo, main channel of Congo River, Les Rapides, near Djoué River confluence — AMNH 239316, (ex. 9), 2C&S, Democratic Republic of Congo, near Inga rapid.

Teleogramma gracile: MCZ 50252, (ex. 8), Democratic Republic of Congo, mainstream near Bulu, W of Luozi. — MCZ 50315, (ex. 8), Democratic Republic of Congo, mainstream at Tadi, near Kibunzi. — AMNH 246716, (ex. 3), Democratic Republic of Congo, Congo River at Lenga Lenga, near first chutes beyond Pioka. — AMNH 240919, (ex. 6), Democratic Republic of Congo, Congo River at Bulu. — AMNH 249892 (ex. 25), 2 C&S, Democratic Republic of Congo, Luozi region, right bank of Congo River.

Teleogramma monogramma: AMNH 12384, (ex. 5), 1 C&S, Democratic Republic of Congo, Luluabourg, Lulua River. — AMNH 253127 (ex. 2), Democratic Republic of Congo, Tshimbadi, Lulua River. — AMNH 247819, (ex. 10), Democratic Republic of Congo, Katende, Lulua River. — AMNH 247806, (ex. 1), AMNH 247818, (ex. 4), Democratic Republic of Congo, Bunkonde, Lulua River. — AMNH 247780, (ex. 5), Democratic Republic of Congo, Nsanga Nyembo, Lulua River. — AMNH 247821, (ex. 3), 3 C&S, Democratic Republic of Congo, Bunkonde Lulua, River.

DISCUSSION

Most cichlid species diversity in the LCR and lower reaches of the middle Congo River is concentrated around, and often restricted to, shoreline rocky outcrops (see, e.g., fig. 2). Such habitat patches are extremely common along much of the length of the LCR. While they are less prevalent upstream of Pool Malebo, a number of them are interspersed between long stretches of sand or grass and reed-covered shoreline along the lower reaches of the middle Congo River.

As previously noted, all specimens of *T. obamaorum* were found at a time of record low water when they were collected upstream of Pool Malebo among rocks newly exposed at the water surface and extending from the shoreline into the main channel of the middle Congo River. Numerous collections had been made along these shorelines in previous (and subsequent) years when water levels were at standard depths, but no specimens of *T. obamaorum* were collected. It would appear then that *T. obamaorum* is likely restricted to deepwater, rocky habitats that typically remain submerged well below the water surface, but became exposed and accessible for sampling during the exceptionally low water stand of 2011. It is noteworthy that in these same, rarely exposed habitats, we also collected representatives of three species that had previously been considered to be endemic to rocky outcrops of the LCR (Lowenstein et al., 2011): *Chrysichthys helicophagus*, *Platyallabes tihoni*, and *Mastacembelus simbi*.

Our inference that *T. obamaorum* is restricted to deepwater rocky habitats is supported by its markedly inflated canals and pores in the laterosensory system of the head, jaws, suspensorium and infraorbital series. These are features associated with enhanced sensory acuity in diverse lineages of deepwater lake cichlids (Fryer and Iles, 1972; Webb et al., 2008), and not found in other species of *Teleogramma*.

Examination of gut contents suggests that *Teleogramma* congeners are almost exclusively insectivorous, feeding on aquatic larvae and nymphs, primarily ephemeropterans but also, to a lesser extent, trichopterans, plecopterans, and chironomids extracted from rock surfaces and interstices. In contrast, the diet of *T. obamaorum* consists almost exclusively of rissooidean gastropods (fig. 8). It seems probable that at depth, *Teleogramma obamaorum* utilizes its enhanced laterosensory system for prey location (Webb et al., 2014), selectively extracting the small gastropods from among rocks deep in the water column. While all shells retrieved from guts appear intact, it is likely that *T. obamaorum* utilizes its robust pharyngeal jaw apparatus and relatively massive LPJ dentition to manipulate and slightly fracture the shells before passing them to the digestive tract for enzymatic breakdown of soft tissue. Because the shells are not dismantled during processing and transport, and must be accommodated along the entire length of the gut, the characteristically expansive distal limb of the intestine observed in *T. obamaorum* (fig. 7A), but absent in insectivorous congeners, may represent an additional trophic adaptation serving to accommodate empty snail shells prior to extrusion.

As noted above the lack of sexual dichromatism in *T. obamaorum* is distinctive within the genus. The lower and middle Congo River carry a heavy sediment load, with high turbidity and intense humic coloring derived from the upstream Cuvette Centrale (Roberts and Stewart, 1976), and light attenuates rapidly from between 0.5 to 1 m below the surface (personal obs.). Under these circumstances, color vision at depth is likely to be extremely limited, and we speculate that this difference in habitat depth occupancy may account for the lack in *T. obamaorum* of the sexual dichromatism common to all its congeners (Roberts and Stewart, 1976).

The discovery of a new, ecomorphologically specialized *Teleogramma* species from the lower reaches of the middle Congo River underscores the highly specialized nature of this unusual clade of riverine cichlids. While the range of phenotypic and ecological diversity exhibited by members of the hyperdiverse cichlid assemblages of the East African Great Lakes con-

tinues to inspire interest in the processes and mechanisms underpinning these remarkable lacustrine radiations (e.g., Santos and Salzberger, 2012; Brawand et al., 2014), considerably less attention has been focused on the evolutionary dynamics of riverine cichlids (but see Markert et al., 2010; Schwarzer et al., 2011). However, the high degree of morphological specialization described in the present study, in addition to previous work highlighting the importance of standing variation in ancestral riverine lineages (Brawand et al., 2014), suggest that a deeper understanding of riverine cichlids, particularly those exhibiting specialized ecologies and morphologies, will yield unique insights into diversification processes in the Cichlidae. In particular, an in-depth analysis of evolutionary dynamics in riverine cichlids such as *Teleogramma* may help determine whether genomic (e.g., gene duplication) and ecomorphological features associated with lacustrine radiations are common to cichlids across environmentally disparate habitats and of varying evolutionary ages. Ongoing efforts to develop genomic resources for several African riverine genera (including *Teleogramma* and *Lamprologus*) hold great potential to improve understanding of the genomic mechanisms that generate the extraordinary morphological diversity found among cichlids.

ACKNOWLEDGMENTS

For assistance with permits and logistical support during collecting trips to the Democratic Republic of Congo we extend our thanks to Julien Punga Kumanenga, Jean Malekani Mukulire, and Koffi Mulumba (University of Kinshasa, and Ministry of Agriculture, D.R. Congo). For companionship and assistance in the field we are grateful to our Congolese colleagues Victor Mamonekene (University of Marien Ngouabi), Raoul Monsembula Iyaba, Tobit Liyandja, and José Justin Mbimbi Mayi Munene (University of Kinshasa). We are particularly grateful to David Grimaldi (Entomology, AMNH), Ellinor Michel, and Jon Todd (Malacology, Natural History Museum, London) for their generous help and expertise with stomach-contents identification. At the AMNH Jairo Arroyave provided helpful input on an earlier draft of this manuscript, Helen Sarakova assisted with numerous aspects of the study, and Barbara Brown, Radford Arrindell, and Lowell Flanders are acknowledged for the curation and care of specimens examined in the study. We thank Bianca Brown (York College/CUNY) for her assistance in genetic data collection and analysis. This contribution benefited from the helpful comments of Richard Vari (Smithsonian Institution) and Kevin Conway (Texas A&M University).

Funds from the Axelrod Research Curatorship, PSC-CUNY, and a generous gift from Ms. Janine Luke provided financial support for this study.

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