

A new small barb (Cyprininae: Smiliogastrini)
from the Louesse, Lekoumou (upper Niari basin),
and Djoulou (upper Ogowe basin) rivers in the
Republic of Congo, west-central Africa

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ABSTRACT

A new species of smiliogastrin cyprinid is described from the Louesse, Lekoumou (upper Niari basin), and Djoulou (upper Ogowe basin) rivers in the Republic of Congo, west-central Africa. The new species is readily distinguished from congeners by the presence of a flexible, weakly ossified and smooth bordered last unbranched dorsal-fin ray, well-developed barbels, and a straight and complete lateral line in combination with a characteristic pigmentation patterning consisting of a distinctive, rounded black spot at the base of and extending over the first rays of the anal fin and a prominent, darkly pigmented blotch over the base of the anterior dorsal-fin rays. A combination of morphological features and pigmentation patterning that appears to be unique among *Enteromius*. The new species is widespread throughout the Louesse-Djoulou region, and the fact that such a seemingly common species has gone undetected until now serves to underscore how poorly known this region of the Republic of Congo remains.

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INTRODUCTION

In a report on a collection of fishes from the Lekoumou River, a southern tributary of the Louesse River in the Republic of Congo, Mamonekene and Stiassny (2012a) noted the presence of two small barbs (Cyprininae; Smiliogastrini) that they considered undescribed species. In a later checklist of fishes from the region Mamonekene and Stiassny (2012b: table 2, fig. 6B) indicated an extended range for the nominal species originally designated as *Barbus* sp. 2, and illustrated specimens in both life and preservation. Since that report was published additional collections from the upper Niari and upper Ogowe river basins have rendered considerably more specimens of that nominal species, as well as additional material of all other small barbs reported for the region. Based on these, in addition to comparative materials and a review of relevant literature, we describe the species initially designated as *Barbus* sp. 2 by Mamonekene and Stiassny (2012a).

Yang et al. (2015) recently proposed the generic name, *Enteromius*, to accommodate many of the small smiliogastrin barbs of Africa and while controversy exists regarding the naming of such a patently paraphyletic grouping (see discussion in Schmidt and Bart, 2015; Stiassny and Sakharova, 2016), Hayes and Armbruster (2017) have argued for the practical utility of its adoption. The authoritative *Catalog of Fishes* (Eschmeyer et al., 2018) and a growing number of taxonomists (e.g., Decru et al., 2016; Lederoun and Vreven, 2016; Skelton, 2016; Van Ginneken et al., 2017) have adopted the name. Following this practice, we have chosen to assign the new species described here to the genus *Enteromius*.

MATERIALS AND METHODS

Fourteen morphometric measurements and 16 meristic counts were taken following Lévêque et al. (1987). Specimens were pinned flat, and photographed on the left side with a Nikon Digital SLR camera and 60 mm f/2.8 AF Micro-Nikkor lens. Linear measurements were taken using the open access software ImageJ v1.48 (Schneider et al., 2012). Vertebral and fin-ray counts were taken from radiographed and/or cleared and stained specimens. Last branched + $\frac{1}{2}$ ray of the dorsal and anal fins articulating with the same pterygiophore were counted as a single element. Vertebral counts include the four Weberian centra and the compound terminal centrum. Lateral-line counts exclude the pored scales distal to the point of caudal flexion. Gill-raker counts correspond to the total number of rakers arrayed along the ceratobranchial and epibranchial elements of the first arch.

Abbreviations used are: AMCC, Ambrose Monell Cryo Collection of the American Museum of Natural History; C&S, cleared and stained specimens; SL, standard length, HL, head length. Institutional abbreviations follow Sabaj (2016).

Except for *E. catenarius*, for which no tissue samples are available, total genomic DNA was extracted from exemplars of all *Enteromius* collected from the Louesse-Djoulou region. Amplification and sequencing of partial cytochrome *c* oxidase subunit I (COI) was carried out as described in Stiassny et al. (2016). Contig assembly and sequence editing were performed using Geneious Pro v11.1.5 (Biomatters, available from <http://www.geneious.com/>). A distance

TABLE 1. Distance matrix indicating percentage of identity in partial cytochrome *c* oxidase subunit I (COI) sequences for representatives of 15 of the 16 smiliogastrins reported by Mamonekene and Stiasny (2012b) from the surveyed region; bottom row indicates values for *E. castrasibutum* (see text). Where no intraspecific variation in COI sequence was found a single individual is represented in the matrix.

	<i>E. kuilu-ensis</i>	<i>E. kuilu-ensis</i>	<i>E. mar-torelli</i>	<i>E. prion-acanthus</i>	<i>E. rouxi</i>	<i>E. rubro-stigma</i>	<i>E. trispilo-mimus</i>	<i>E. walshae</i>	<i>E. nigro-luteus</i>	<i>E. brich-ardi</i>	<i>E. campta-canthus</i>	<i>E. chium-beensis</i>	<i>E. diam-ouanganai</i>	<i>E. guirali</i>	<i>E. holotaenia</i>	<i>E. jae</i>
<i>E. kuiluensis</i>																
<i>E. kuiluensis</i>	0.3															
<i>E. martorelli</i>	2.0	2.0														
<i>E. prionacanthus</i>	6.6	6.3	6.9													
<i>E. rouxi</i>	14.8	14.8	14.8	15.4												
<i>E. rubrostigma</i>	6.0	6.0	5.9	6.5	15.0											
<i>E. trispilomimus</i>	12.8	13.0	13.7	13.7	13.4	12.2										
<i>E. walshae</i>	10.5	10.2	10.8	11.3	14.4	11.1	12.2									
<i>E. nigroluteus</i>	14.2	14.4	13.9	14.2	15.4	13.9	12.0	12.8								
<i>E. brichiardi</i>	9.9	9.6	10.2	10.2	15.0	10.5	11.7	5.9	13.0							
<i>E. camptacanthus</i>	7.1	7.1	7.7	7.4	14.0	8.5	11.3	9.7	12.3	8.2						
<i>E. chiumbeensis</i>	9.9	9.6	9.6	10.0	13.3	9.1	12.7	9.3	14.0	10.2	8.2					
<i>E. diamouanganai</i>	4.9	4.9	4.9	7.9	13.7	5.9	12.5	10.3	13.4	10.3	7.4	9.0				
<i>E. guirali</i>	4.3	4.0	4.6	5.9	14.7	4.8	11.7	10.3	13.0	9.7	7.4	8.8	4.5			
<i>E. holotaenia</i>	5.2	4.9	5.6	7.7	14.7	6.2	12.5	10.6	13.3	9.6	7.7	9.6	2.2	3.5		
<i>E. jae</i>	13.6	13.7	12.7	13.7	14.2	12.7	12.3	11.6	3.4	12.3	11.6	12.8	12.3	12.2	12.3	
<i>E. castrasibutum</i>	14.0	13.7	14.2	13.3	15.6	14.2	15.1	11.3	15.6	12.0	12.8	13.6	13.9	13.0	14.2	15.3

matrix indicating the percentage of identity in COI sequence between sampled taxa is given in table 1. Images of species exemplars photographed immediately postmortem or in preservation are given in figure 1. Specimen voucher catalog numbers, individual tissue codes, and GenBank accession numbers for sequences generated in this study are provided in table 2.

Given the highly speciose nature of the genus *Enteromius*, with more than 200 species currently recognized (Hayes and Armbruster, 2017), direct comparison with all described species is not practicable. In the current study, initial morphological (and COI barcode) comparison was made with congeners known from the Louesse, Lekoumou, and Djoulou river basins and then, via literature review (Stiassny et al., 2007), was extended to the entire lower Guinean ichthyofaunal province, of which the Kouilou-Nairi and upper Ogowe basins form the southern region. Further review of literature documenting *Enteromius* diversity in the lower and middle Congo (Lowenstein et al., 2010; Monsembula Iyaba et al. 2013, Ibala Zamba, 2010; Monsembula Iyaba and Stiassny, 2013), Angola (Poll, 1967), Ubangi basin (Gosse, 1968), western (Paugy et al., 2003) and southern Africa (Skelton, 2001), extended the geographical scope of comparisons into all proximal ichthyofaunal provinces.

***Enteromius walshae*, new species**

Figures 2, 3; table 3

HOLOTYPE: AMNH 266856, female, 52.7 mm SL, Republic of Congo, Niari Province, Mayoko County, Tributary of Mandoro River (2°17'38.6" S, 12°51'56.8" E), G. Walsh et al., 10 January 2012.

PARATYPES: AMNH 266857, 3 specimens, 1 C&S, 41.3–51.2 mm SL, same data as holotype. — AMNH 266805, 5 specimens, 30.1–43.2 mm SL, same locality as the holotype, G. Walsh et al., 18 October 2013. — OS 22280, 2 specimens, 49.7–50.1 mm SL, Republic of Congo, Niari Province, Mayoko County, Tributary of Mandoro River (2°17'57.3" S, 12°46'6.2" E), G. Walsh et al., October 2013. — MRAC 2018-027-P-0001-0002, 2 specimens, 36.8–37.1 mm SL, Republic of Congo, Niari Province, Mayoko County, Tributary of Mandoro River (2°19'07" S, 12°49'46" E), G. Walsh et al., October 2013. — ZSM 47362, 2 specimens 31.6–38.5 mm SL, Republic of Congo, Lekoumou River at bridge (3°22'49.3" S, 13°15'55.0" E), V. Mamonekene, 8 December 2010. — AMNH 266858, 2 specimens, 42.5–51.1 mm SL, Republic of Congo, Niari Province, Tsinguidi County, Loula River (2°26'48.9" S, 12°58'21.9" E), G. Walsh et al., 18 November 2013. — AMNH 266806, 4 specimens, 36.1–53.7 mm SL, Republic of Congo, Niari Province, Tsinguidi County, Tributary of Mandoro River (2°24'24.1" S, 12°56'55.0" E), G. Walsh et al., 13 November 2013. — AMNH 266808, 2 specimens, 34.0–52.1 mm SL, Republic of Congo, Niari Province, Tsinguidi County, Tributary of Mandoro River (2°25'27.2" S, 12°53'19.8" E), G. Walsh et al., 18 October 2013. — AMNH 266859, 3 specimens, 28.2–41.3 mm SL, Republic of Congo, Niari Province, Mayoko County, Louesse River (2°14'29.5" S, 12°47'38.3" E), G. Walsh et al., 10 January 2012. — AMNH 266860, 6 specimens, 3 C&S, 31.1–40.5 mm SL, Republic of Congo, Niari Province, Mayoko County, Lekoumou River at bridge (3°22'49.3" S, 13°15'55.0" E), V. Mamonekene, 8 December 2010. — AMNH 266861, 4

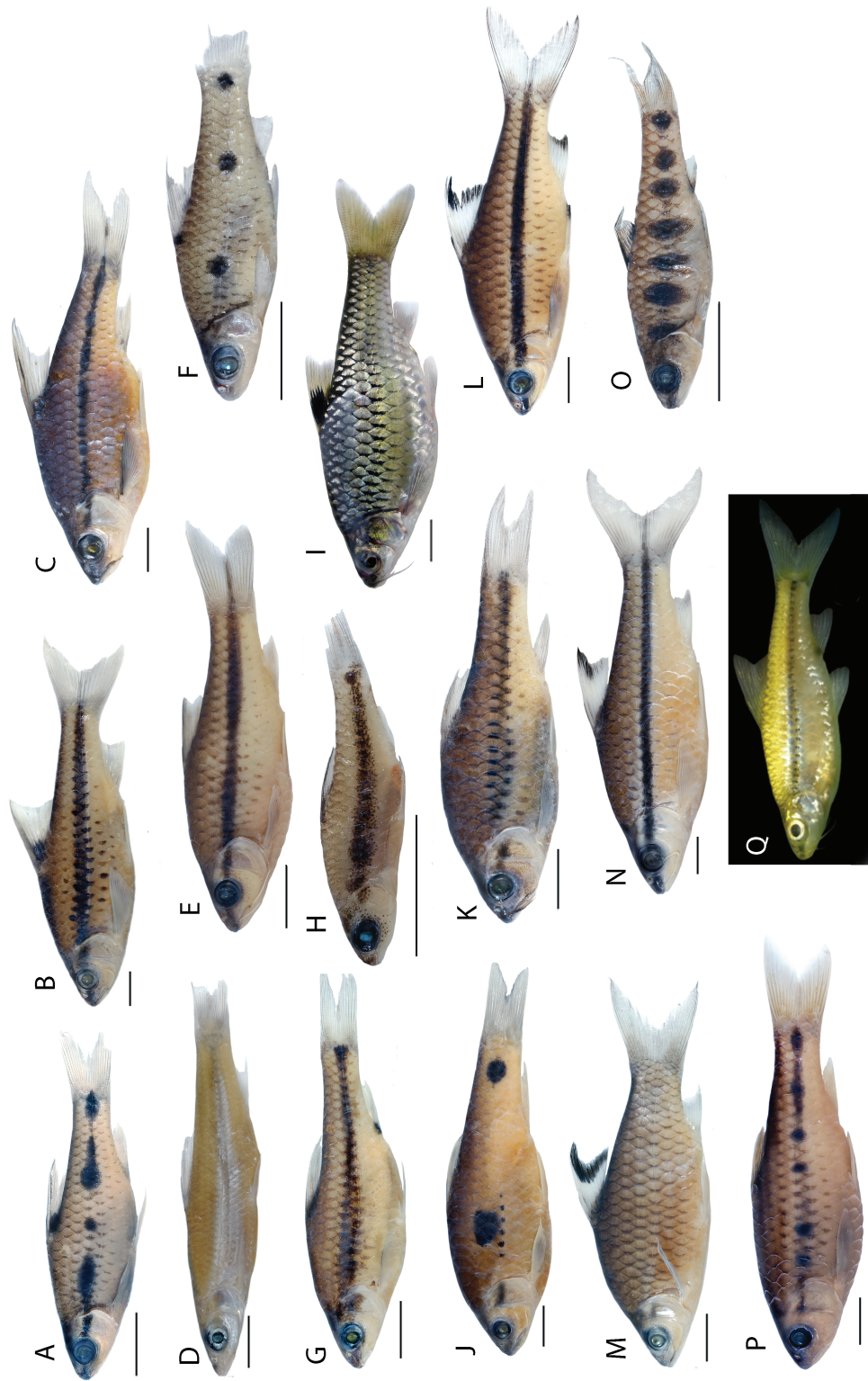


FIGURE 1. *Enteromius* species sampled (table 1), photographed immediately postmortem or in preservation: A, *kuiluensis*; B, *martorelli*; C, *prionacanthus*; D, *rouxi*; E, *rubrostrigatus*; F, *trispilomimus*; G, *walsbaei* new species; H, *nigroluteus*; I, *brichardi*; J, *camptacanthus*; K, *chiumbeensis*; L, *diamounanganai*; M, *guirali*; N, *holotaenia*; O, *jai*; P, *catenarius*; Q, *castrasibutum*. No tissues are currently available for *E. catenarius*. Photograph of *E. castrasibutum* courtesy of Jon Armbruster.

TABLE 2. Taxa, voucher catalog numbers, and GenBank accession numbers for COI sequences obtained in this study.

Taxon	AMNH catalog	Tissue code	COI
<i>Enteromius brichardi</i>	AMNH 254008	AMCC 236033	MK033116
<i>Enteromius camptacanthus</i>	AMNH 256531	AMCC 221806	MK033117
<i>Enteromius camptacanthus</i>	AMNH 258475	AMCC 211928	MK033118
<i>Enteromius chiumbeensis</i>	AMNH 258901	AMCC 211958	MK033119
<i>Enteromius chiumbeensis</i>	AMNH 256530	AMCC 221795	MK033120
<i>Enteromius diamouanganai</i>	AMNH 253883	AMCC 236036	MK033121
<i>Enteromius guirali</i>	AMNH 254006	AMCC 236030	MK033122
<i>Enteromius guirali</i>	AMNH 253941	AMCC 236139	MK033123
<i>Enteromius holotaenia</i>	AMNH 258385	AMCC 211614	MK033124
<i>Enteromius holotaenia</i>	AMNH 258144	AMCC 211415	MK033125
<i>Enteromius jae</i>	AMNH 253987	AMCC 235986	MK033126
<i>Enteromius kuiluensis</i>	AMNH 253891	AMCC 236133	MK033103
<i>Enteromius kuiluensis</i>	AMNH 253891	AMCC 253122	MK033104
<i>Enteromius martorelli</i>	AMNH 253985	AMCC 236065	MK033105
<i>Enteromius nigroluteus</i>	AMNH 253888	AMCC 236135	MK033114
<i>Enteromius nigroluteus</i>	AMNH 253888	AMCC 236136	MK033115
<i>Enteromius prionacanthus</i>	AMNH 258881	AMCC 211985	MK033106
<i>Enteromius prionacanthus</i>	AMNH 256523	AMCC 221799	MK033107
<i>Enteromius rouxi</i>	AMNH 253939	AMCC 236138	MK033108
<i>Enteromius rubrostigma</i>	AMNH 264335	AMCC 235826	MK033109
<i>Enteromius rubrostigma</i>	AMNH 264335	AMCC 235827	MK033110
<i>Enteromius trispilomimus</i>	AMNH 254007	AMCC 236031	MK033111
<i>Enteromius walshae</i> , n. sp.	AMNH 256534	AMCC 221826	MK033112

specimens, 38.2–53.2 mm SL, Republic of Congo, Niari Province, Mayoko County, Bakoulou River (2°16'58.6" S, 12°48'23.3" E), G. Walsh et al., 10 January 2012. AMNH 266862, 5 specimens, 2 C&S, 36.1–53.2 mm SL, Republic of Congo, Niari Province, Djoulou River at bridge (2°33'31.8" S, 13°34'30.0" E), V. Mamonekene, 4 December 2010.

DIFFERENTIAL DIAGNOSIS: While no unambiguous morphological autapomorphies have been located to diagnose *Enteromius walshae* the species is nonetheless readily distinguished from all congeners by the presence of a flexible, weakly ossified, and smooth-bordered last unbranched dorsal-fin ray, well-developed barbels, and a straight and complete lateral line in combination with a characteristic pigmentation patterning consisting of a distinctive, rounded black spot at the base of and extending over the first rays of the anal fin and a prominent, darkly pigmented blotch over the base of the anterior dorsal-fin rays.

DESCRIPTION: A small *Enteromius* species attaining a maximum recorded size of 53.7 mm SL (mature female, AMNH 266806), with general appearance as in figure 2. (See table 3 for proportional measurements and meristic counts for the holotype and 40 paratypes.) Body

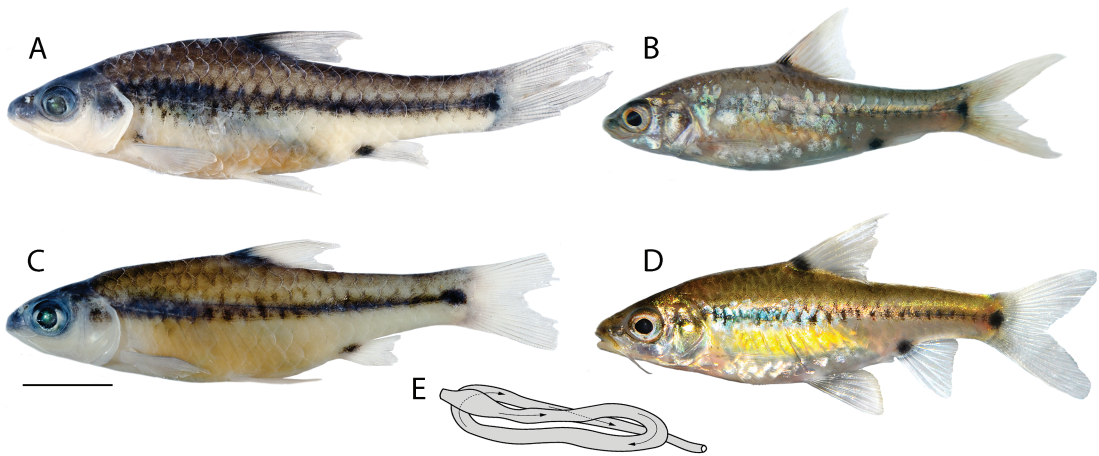


FIGURE 2. *Enteromius walshae*, new species: **A**, AMNH 266856, holotype (female) in preservation; **B**, individual from the same population in life. **C**, AMNH 266858, paratype (male) in preservation; **D**, individual from same population in life; **E**, digestive tract, after removal of liver and adherent tissues (approximately to scale).

moderately elongate, laterally compressed, although belly of ripe females often distended. Head small, eyes large, mouth subinferior, two pairs of barbels. In smaller specimens (<35 mm SL) maxillary barbels extend to anterior third of eye, mandibular pair reach just beyond posterior margin of orbit. In larger specimens, maxillary pair extends posterior to level of mideye, mandibular pair reaches anterior border of preopercle. No tubercles or sensory pit lines present. Cranium fully ossified with no open occipital fontanel. Five infraorbitals (IO): IO1 deepest of the series, IO2–5 tubular (compare panel A with panels B and C of fig. 3), with medially located infraorbital canal. Scales radially striated, 23–26 in lateral line (+1–2 over caudal-fin base), 4.5/1/3.5 transverse body rows, 11 circumpeduncular rows (rarely 12), 8.5–9.5 predorsal scale rows. Lateral line complete, located along midline with pored scales not enlarged relative to those along impinging rows above and below.

Dorsal fin iii.8, positioned midway between snout and caudal-fin base, origin at, or slightly anterior to, pelvic-fin insertion. Last unbranched ray long and weakly ossified, segmented distally, and lacking serrations along posterior border (fig. 3D). Anal fin iii.5 (rarely iii.6), forked caudal fin, 9 + 10 principal rays, 6–8 + 7–9 procurent rays. Pelvic fin i.7, pectoral fin i.12–13. Gill rakers small, 4–6 restricted to distal portion of ceratobranchial and epibranchial of first arch.

Total vertebrae 30–31, 16–17 abdominal, 14–15 caudal (holotype 31, 17+14). Eleven or 12 pleural ribs, 4 (rarely 5) broad supraneurals located between and filling the interspaces of neural spines of vertebral centra 4–8 (compare fig. 3D and E). First dorsal-fin pterygiophore between neural spines of vertebral centrum 8–9, and first anal-fin pterygiophore directed at hemal spine of vertebral centra 17–19. Caudal-fin rays supported by neural and hemal spines of preural centra 2–3. Pleurostyle, single epural, parhypural + seven hypural elements present.

COLORATION: In preservation (fig. 2A, C), base body coloration cream or creamy yellow, darker dorsally, becoming paler ventrally over belly, cheeks, and lower jaws. Snout and dorsum of head heavily pigmented and dark, opercular blotch usually well developed. Prominent lateral

TABLE 3. Morphometric measurements and meristic data for the holotype and 40 paratypes of *Enteromius walshae*, new species. Mean values exclude measurements of the holotype.

Morphometric measurements	Holotype	Paratypes			
		min	max	n	mean
Standard length (mm)	52.7	28.2	53.7	40	
% SL					
Head length	26.4	24.5	28.3	25	26.2
Predorsal length	49.8	48.0	50.9	25	49.6
Prepectoral length	29.0	27.2	32.2	25	29.4
Prepelvic length	47.8	47.1	51.8	25	49.0
Preanal length	72.8	70.6	74.5	25	72.8
Dorsal-fin base	13.3	13.2	16.1	25	14.2
Anal-fin base	6.8	6.5	9.2	25	7.7
Caudal peduncle depth	12.5	12.2	13.5	25	12.8
Body depth	29.1	26.1	31.5	25	29.5
% HL					
Eye diameter	30.6	28.4	38.1	25	32.8
Lower jaw length	38.2	34.3	46.1	25	40.8
Maxillary length	29.0	24.4	30.4	25	27.4
Snout length	30.5	27.1	30.7	25	29.1

Meristic counts	holotype	Paratypes
Gill rakers (total) on first arch	5	5(23), 6(2)
Lateral line scales	24	23 (10), 24(12), 25(2), 26(1)
Lateral line-dorsal fin scale-rows	4.5	4.5(25)
Lateral line-pelvic fin scale-rows	3.5	3.5(25)
Predorsal scales	9	8.5(3), 9(15), 9.5(2)
Circumpeduncular scale-rows	11	11(15), 12(5)
Dorsal-fin rays	iii-8	iii.8(25)
Anal-fin rays	iii-5	iii.5(23), iii.6(2)
Abdominal vertebra	17	16(2), 17(19)
Caudal vertebra	14	14(12), 15(9)
Total vertbrae	31	30 (12), 31(9)
Pleural ribs	12	11(3), 12(16)
Principal caudal-fin rays	9+10	9+10(25)
Procurent caudal-fin rays	7+8	6+7(2), 7+8(8), 8+9(5)
Pelvic-fin rays	i.7	i.7(15)
Pectoral-fin rays	i.13	i.13(12), i.14(3)

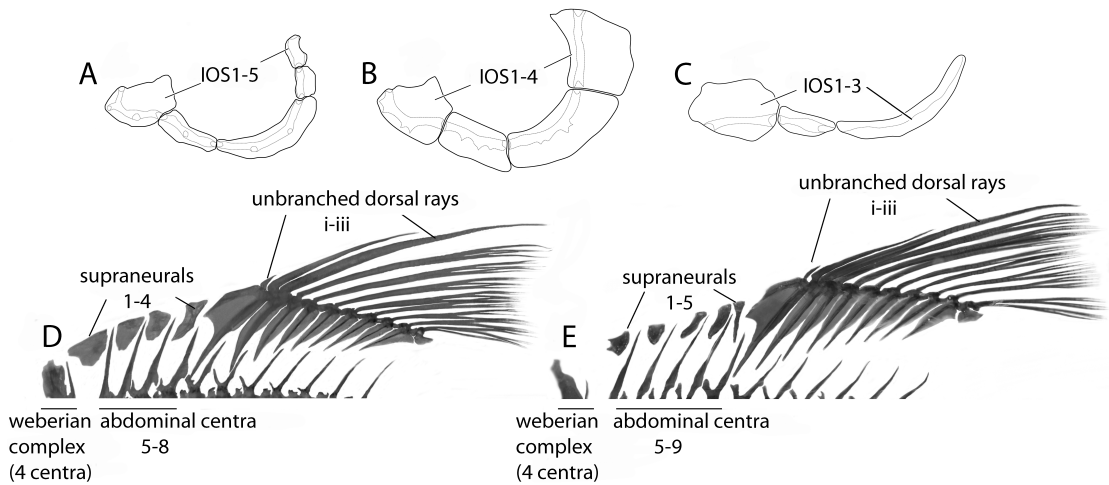


FIGURE 3. Isolated infraorbital series: **A**, *E. walshae* (AMNH 266860); **B**, *E. camptacanthus* (AMNH 256416); **C**, *E. jae* (AMNH 253857). Anterior vertebrae, dorsal fin, and associated supraneural elements; **D**, *E. walshae* (AMNH 266862); **E**, *E. catenarius* (AMNH 266868).

band overlies a somewhat zigzag-patterned midlateral scale series. Lateral band widest anteriorly, becoming somewhat attenuated posteriorly, terminating in round or ovoid caudal spot over line of caudal flexion, not extending onto caudal fin. Darkly pigmented blotch over base of anterior dorsal-fin rays. Prominent, rounded black spot at anterior base of, and extending onto, first few anal-fin rays. Fins otherwise pale gray or hyaline. Base coloration in life somewhat variable, either predominately silvery (fig. 2B) or golden (fig. 2D). Opercular blotch and midlateral band only faintly visible, black pigmentation at anterior base of dorsal, anal and caudal fins strongly marked.

GUT MORPHOLOGY AND DIET: Digestive tract long and looped; esophagus leads to small, thin-walled stomach. Intestine exits directly from distal end of stomach, forms primary loop passing posteriad almost to anus, looping back antieriad to pass under stomach forming a secondary loop extending posteriad to anus (fig. 2E). Total length of tract (unraveled but not stretched) ca. 1.3–1.5 times SL. Review of gut contents in preserved specimens indicates *E. walshae* feeds principally on detritus and organic debris. Guts contain detritus, sand grains, some chironomid larval head cases and other fragmented, unidentifiable insect remains.

REPRODUCTION: Sexually mature at small size; largest female containing ripe eggs, 32.5 mm SL (AMNH 258816). Adult females generally attaining larger sizes than males (largest female, 53.7 mm SL, AMNH 266806; largest male, 51.0 mm SL, AMNH 266807). Most individuals collected October–February had ovaries filled with numerous small, round eggs or enlarged testes, suggesting a protracted reproductive period at commencement of and during rainy season. Water levels are high and water is extremely turbid in large rivers during this period; however, most specimens were collected in small, forested streams where water levels remain low throughout most of the rainy season.

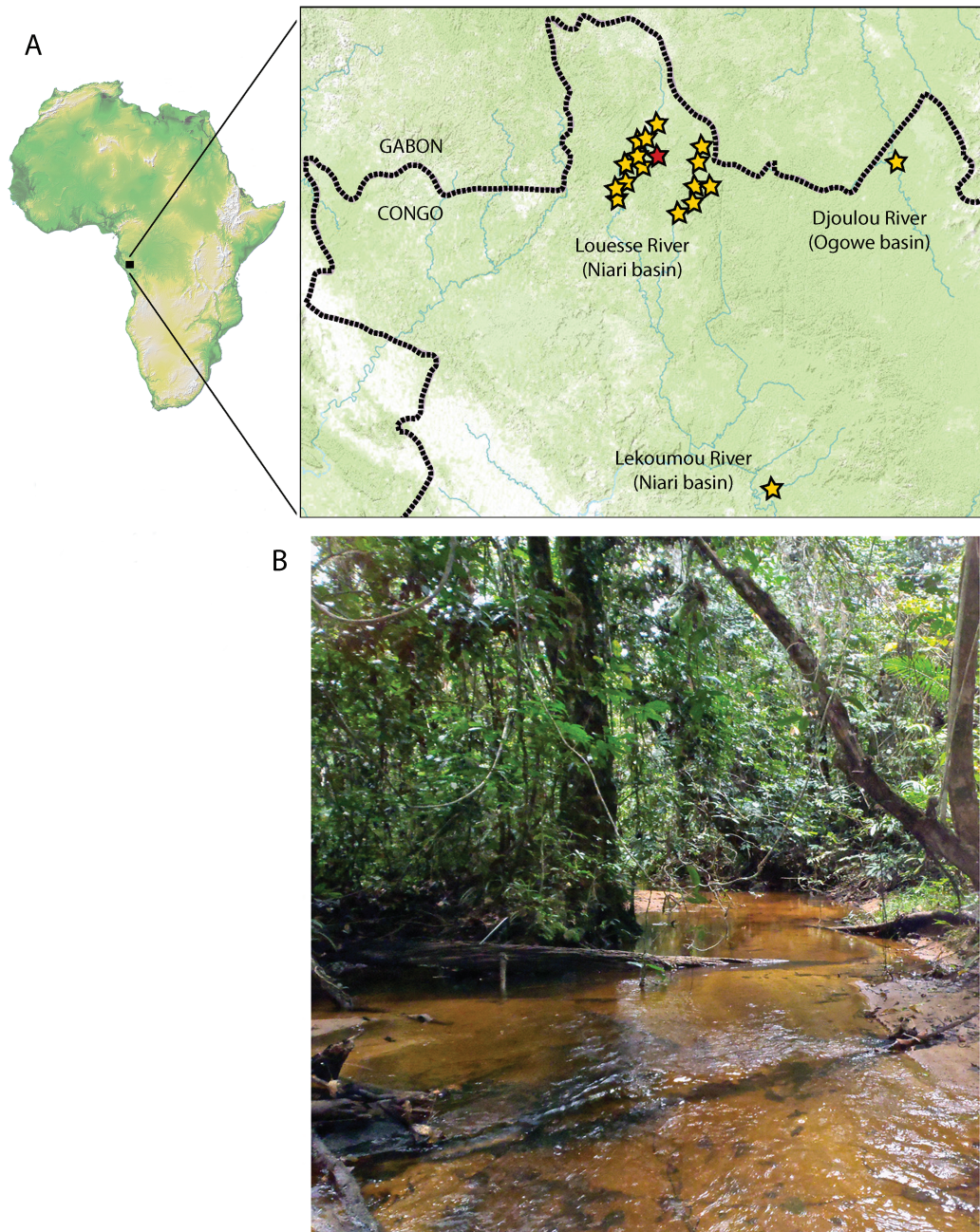


FIGURE 4. **A**, Known distributional range of *Enteromius walshae*; yellow stars indicate collection sites and red star indicates collection locality of holotype (AMNH 266856). **B**, Type locality of holotype, in a small tributary of the Mandoro River (upper Louesse River basin).

DISTRIBUTION: Found in forested streams and rivers throughout the surveyed region (fig. 4A). Commonly encountered in tributaries and subtributaries of the Louesse River in the Niari basin, and in the Djoulou River, a tributary of the upper Ogowe. The species is not found in tributaries of the lower Kouilou-Niari or in coastal basin systems in the Republic of Congo (Walsh et al., 2014). Although no data are currently available, we anticipate that further collecting in the upper Ogowe basin will extend the species' distributional range into adjacent forested regions of that basin in Gabon.

ETYMOLOGY: We name this new smiliogastrin cyprinid for our colleague Gina Walsh (University of Witwatersrand, South Africa), whose ongoing research continues to enhance conservation efforts throughout the region.

COMPARATIVE MATERIALS EXAMINED: *Enteromius atakorensis*: AMNH 226419, 4 specimens, Guinea, Creek crossing highway between Parakou and Ndali.

Enteromius atromaculatus: AMNH 6295, holotype, Democratic Republic of Congo, Yakuluku Port, Uele River, Ubangi basin.

Enteromius barotseensis: AMNH 269055, 4 specimens, Democratic Republic of Congo, Lulua River at Kayala (7°44'21.7"S, 22°36'39.6" E).

Enteromius baudoni: AMNH 257020, 6 specimens, Guinea (9°46'56.4" S, 10°38'06.9" E).

Enteromius bifrenatus: AMNH 269058, 28 specimens, Democratic Republic of Congo, Lulua River 150 km from Angolan border (9°42'43.2" S, 22°51'11.4" E).

Enteromius brichardi: AMNH 254008, 1 specimen, Republic of Congo, Niari Province, Passi-Passi River (3°51'58.4" S, 12°20'47.2" E).

Enteromius camptacanthus: AMNH 256531, 6 specimens, Republic of Congo, Niari Province, Mandoro River (2°17'59.2" S, 12°51'59.1" E). — AMNH 256416, 8 specimens, 2 C&S, Republic of Congo, Niari Province, Mayoko County, Tributary of Mandoro River (2°19'37.4" S, 12°49'58.8" E).

Enteromius catenarius: AMNH 266863, 8 specimens, 1 C&S, Republic of Congo, Bouenza Province, Nkendala River, near Boko Songho. — AMNH 266868, 6 specimens, 1 C&S, Republic of Congo, Bouenza Province, Bodi River, near Boko Songho.

Enteromius chiumbeensis: AMNH 258901, 19 specimens, Republic of Congo, Niari Province, Mayoko County, Tributary of the Mandoro River (2°19'06.9" S, 12°49'46.7" E). — AMNH 256477, 11 specimens, 2 C&S, Republic of Congo, Niari Province.

Enteromius diamouanganai: AMNH 263062, 6 specimens, Republic of Congo, Kouilou Province, Kigongo River (4°33'39.5" S, 12°06'30.4" E). — AMNH 263139, 2 specimens, Republic of Congo, Kouilou Province, Mambana River (4°32'53.3" S, 12°06'01.5" E). — AMNH 253883, 1 specimen, Republic of Congo, Kouilou Province, Kouilou-Niari River at Sounda (4°04'48.5" S, 12°08'18.4" E).

Enteromius guirali: AMNH 253881, 4 specimens, Republic of Congo, Kouilou Province, Kouilou-Niari River at Sounda (4°04'48.5" S, 12°08'18.4" E). — AMNH 253941, 2 specimens, Republic of Congo, Niari Province, Kouilou-Niari River at Loudima (4°06'01.0" S, 13°03'38.0" E).

Enteromius haasianus: AMNH 269072, 2 specimens, Democratic Republic of Congo, Lulua River 150 km from Angolan border (9°42'43.2" S, 22°51'11.4" E).

Enteromius holotaenia: AMNH 253870, 2 specimens, Republic of Congo, Lekoumou Province, Djoulou River (2°33'31.8" S, 13°34'30.0" E). — AMNH 258144, 6 specimens, Republic of Congo, Kouilou Province, at Tissa (4°8'44.4" S, 11°42'48.1" E) — AMNH 250765, 8 specimens, 2 C&S, Democratic Republic of Congo, Small stream flowing into main channel of the N'Sele (4°26'41" S, 15°41'00" E).

Enteromius jae: AMNH 256447, 1 specimen, Republic of Congo, Lekoumou Province, River Kessampo (2°46'25.9" S, 13°48'56.7" E). — AMNH 253889, 2 specimens, Republic of Congo, Lekoumou Province, Lekoumou River (3°22'49.3" S, 15°48'55.0" E) — AMNH 253857, 29 specimens, 3C&S, Republic of Congo, Djoulou River at bridge (2°33'31" S, 13°34'30" E).

Enteromius kuiluensis: AMNH 253891, 64 specimens, 3 C&S, Republic of Congo, Lekoumou Province, Lekoumou River (3°22'49.3" S, 15°48'55.0" E). — MNHN 1929-0243, syntype, Gabon, Kouilou River.

Enteromius lineomaculatus: AMNH 271043, 2 specimens, Tanzania, Uvinza salt works near Nkwasa (5°5'52.5" S, 30°21'16.2" E).

Enteromius macinensis: AMNH 257726, 4 specimens, Guinea (9°41'36.8" S, 10°9'4.4" E).

Enteromius martorelli: AMNH 253985, 5 specimens, Republic of Congo, Niari Province, Lebaya River (2°39'56.6" S, 13°35'45.0" E). — AMNH 256509, 10 specimens, 2 C&S, Republic of Congo, Niari Province, at Comilog (2°13'27.4" S, 12°49'10.8" E).

Enteromius nigroluteus: AMNH 253888, 5 specimens, Republic of Congo, Lekoumou Province, Lekoumou River (3°22'49.3" S, 15°48'55.0" E).

Enteromius prionacanthus: AMNH 258881, 2 specimens, Republic of Congo, Niari Province, Mandoro River (2°19'53.7" S, 12°49'42.3" E). — AMNH 256523, 17 specimens, Republic of Congo, Niari Province, Louesse River at Mayoko (2°17'23.8" S, 12°47'31.0" E). — AMNH 258473, 1 specimen, Republic of Congo, Niari Province, Leala River (2°13'35.4" S, 12°56'5.1" E). — AMNH 264169, 22 specimens, Republic of Congo, Niari Province, Leala River (2°13'35.4" S, 12°56'35.1" E). — AMNH 258889, 20 specimens, Republic of Congo, Niari Province, Tributary of Mandoro River (2°17'38.6" S, 12°51'56.8" E) — AMNH 256454, 3 specimens, 1 C&S, Republic of Congo, Niari Province, Lipia River (2°17'31.7" S, 12°48'29.5" E). — AMNH 264184, 12 specimens, Republic of Congo, Niari Province, Tributary of Mandoro River, (2°23'46.6" S, 12°55'20" E) — AMNH 264194, 11 specimens, Republic of Congo, Niari Province, Tributary of Mandoro River, (2°23'27.5" S, 12°54'55.7" E).

Enteromius rouxi: AMNH 253939, 1 specimen, Republic of Congo, Niari Province, Kouilou-Niari River at Loudima (4°06'01.0" S, 13°03'38.0" E). — AMNH 253828, 1 specimen, Republic of Congo, Loungou River.

Enteromius rubrostigma: AMNH 264335, 4 specimens, 1 C&S, Republic of Congo, Niari Province, Loula River (2°26'39.2" S, 12°58'13.2" E). — AMNH 253905, 1 specimen, Republic of Congo, Lekoumou Province, Passi-Passi River (3°51'58.4" S, 12°20'47.2" E).

Enteromius stigmatopygus: AMNH 230662, 264 specimens, Chad, Manovo-Gounda National Park, Waula Lagoon.

Enteromius sublineatus: AMNH 256981, 5 specimens, Guinea (9°42'20.2" S, 10°24'42.9" E).

Enteromius trispilomimus: AMNH 263487, 1 specimen, Republic of Congo, Kouilou Province, Kigongo River (4°33'39.5" S, 12°06'30.4" E). — AMNH 254007, 1 specimen, Republic of Congo, Lekoumou Province, Passi-Passi River (3°51'58.4" S, 12°20'47.2" E).

Enteromius walshae: AMNH 266810, 4 specimens, 34.0–52.1 mm SL, Republic of Congo, Niari Province, Mayoko County, Tributary of Mandoro River (2°18'12.7" S, 12°58'28.4" E), G. Walsh et al., 16 October 2013. — AMNH 256505, 7 specimens, Republic of Congo, Niari Province, Mayoko County, Bakoulou River at Mayoko (2°17'28.9" S, 12°47'36.5" E), V. Mamonekene, 3 April 2012. — AMNH 266809, 5 specimens, Republic of Congo, Niari Province, Mayoko County, Mandoro River (2°24'13.9" S, 12°58'9.4" E), G. Walsh et al., 12 November 2013. — AMNH 266811, 9 specimens, Republic of Congo, Niari Province, Mayoko County, Leala River, Tributary of Louesse River (2°13'35.4" S, 12°56'35.1" E), G. Walsh et al., 22 October 2013. — AMNH 258861, 2 specimens, Republic of Congo, Niari Province, Mayoko County, Lekoumoumayoko River, (2°19'37.6" S, 12°47'34.7" E), G. Walsh et al., 10 January 2012. — AMNH 258829, 4 specimens, Republic of Congo, Niari Province, Mayoko County, Lipia River, tributary of Louesse River (2°16'58.2" S, 12°49'8.0" E), G. Walsh et al., 10 January 2012.

Enteromius viviparus: AMNH 263442, 22 specimens, Mozambique, Mameme River (15°52'35.7" S, 34°1'47.4" E).

DISCUSSION

Literature review and examination of comparative materials indicate that a small number of *Enteromius* share with *E. walshae* the presence of a prominent dark spot located on or above the anterior anal-fin rays. In western Africa these taxa include *E. atakorensis*, *E. baudoni*, *E. macinensis*, *E. stigmatopygus*, and *E. sublineatus* and in Angola, southern Africa, and the middle Congo basin *E. atromaculatus*, *E. barotseensis*, *E. bifrenatus*, *E. brevipinnis*, *E. castrasibutum*, *E. greenwoodi*, *E. haasianus*, *E. lineomaculatus*, *E. macrotaenia*, and *E. viviparus*. While these taxa all possess a weakly ossified, flexible, and smooth-bordered last unbranched dorsal-fin ray, none share with *E. walshae* the presence of a prominent, darkly pigmented blotch over the anterior base of the dorsal-fin rays and, except for *E. castrasibutum*, each can be distinguished from *E. walshae* based on a combination of meristic, pigmentation, and squamation attributes (Paugy et al., 2003; Poll, 1967; Skelton, 2001). *Enteromius castrasibutum* was described by Fowler (1936) based on a series of specimens collected near Fort Sibut in the Ubangi-Shari (middle Congo basin), and has recently been reported from the Dja River (Armbruster et al., 2016), a right bank tributary of the Congo River located proximal to the lower Guinean region. While *E. castrasibutum* lacks a prominently pigmented blotch over the anterior dorsal-fin rays it otherwise closely resembles *E. walshae* in body form and meristic counts (Fowler, 1936; and see fig. 1Q). However, comparison of Dja River *E. castrasibutum* (GenBank KF791267) and *E. walshae* (Genbank MK033112) indicate the two taxa are over 11% divergent in COI sequence (table 1), a value that well exceeds the standard threshold of 3% commonly used as an indicator of species-level differentiation (Herbert et al., 2003). Similarly, COI sequence comparisons between *E. walshae* and other *Enteromius* species collected in the Louesse-Djoulou

region (table 1) indicate considerable sequence divergence between each of these morphologically recognized species and *E. walshae*. Of the *Enteromius* co-occurring in the upper Kouilou-Niari/upper Ogowe basin *E. walshae* is closest to *E. brichardi* in COI sequence, although percentage divergence between these two taxa is close to 6% (table 1). Given the limited sampling of *Enteromius* included in the present study, no hypothesis of phylogenetic placement for the new species is proposed. Ultimate resolution of relationships within this large clade of African smiliogastrin cyprinids will require both a considerably broader taxon sampling and increased genomic coverage (Schmidt and Bart, 2015; Ren and Mayden, 2016; Stiassny and Sakharova, 2016).

Traditionally, studies of *Enteromius* have focused on a small set of comparative morphometric and meristic features for the description of new species (Lévêque et al., 1987). In addition to these, attributes considered taxonomically (and potentially phylogenetically) important are the condition of the last unbranched dorsal-fin ray (ossified and rigid vs. weakly ossified and flexible, posterior border either smooth or serrate), presence and length (vs. absence) of barbels, and the configuration of the lateral line (incomplete vs. complete, and passing along or below the midline). To these we would add that variation in the shape and number of infraorbital elements (e.g., fig. 3A, B, C), as well as the shape, number, and location of supraneurals and dorsal fin placement relative to associated vertebral elements (e.g., fig. 3D, E), represent useful features for inclusion in species descriptions, and are potentially informative characters for future phylogenetic analysis.

Among the species collected in the surveyed region (figs. 1, 4) *Enteromius walshae* appears to be extremely common, and has been found among collections from throughout the two basins. The fact that such a seemingly common species has gone undetected until now serves to underscore how poorly known this species-rich region of the Republic of Congo remains. Mamonekene and Stiassny (2012a) note that almost all collecting effort in the region have been undertaken as part of social and environmental impact assessments mandated prior to the implementation of major iron ore mining projects and road and rail development. The irony is not lost on us that it is precisely such major infrastructure projects that will have profound and deleterious impacts on aquatic habitats and aquatic diversity throughout the region.

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REFERENCES

- Armbruster, J.W., C.C. Stout, and M.M. Hayes. 2016. An empirical test for convergence and social mimicry using African barbs (Cypriniformes: Cyprinidae). *Evolutionary Ecology* 30: 435–450.
- Decru, E., T. Moelants, E. Vreven, E. Verheyen, and J. Snoeks. 2016. Taxonomic challenges in freshwater fishes: a mismatch between morphology and DNA barcoding in fish of the north-eastern part of the Congo basin. *Molecular Ecological Resources* 16: 342–352.
- Eschmeyer, W.N., R. Fricke, and R. van der Laan. 2018. Catalog of fishes: genera, species. Online resource (<http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp>), accessed 9 October, 2018.
- Fowler, H.W. 1936. Zoological results of the George Vanderbilt African Expedition of 1934. Part III. The fresh water fishes. *Proceedings of the Academy of Natural Sciences, Philadelphia* 83: 243–335.
- Gosse, J.-P. 1968. Les poisons du bassin de l'Ubangi. *Musée Royal de l'Afrique Centrale, Zoologique* 13: 1–56.
- Hayes, M.M., and J.W. Armbruster. 2017. The taxonomy and relationships of the African small barbs (Cypriniformes: Cyprinidae). *Copeia* 105 (2): 348–362.
- Herbert, P.D.N., S. Ratnasingham, and J.R. de Waard. 2003. Barcoding animal life: cytochrome *c* oxidase subunit 1 divergences among closely related species. *Proceedings of the Royal Society of London B, Biological Sciences* 270: 313–322.
- Ibala Zamba, A. 2010. Faune des poisons des rivières Luki et Lefini (bassin du Congo): diversité et écologie. Ph.D. dissertation, Katholieke Universiteit, Leuven. 430 pp.
- Lederoun, D., and E. Vreven. 2016. *Enteromius vandewallei*, a new species of minnow from the Volta River basin, West Africa (Cypriniformes: Cyprinidae). *Ichthyological Explorations of Freshwaters* 27: 97–106.
- Lévêque, C., G.G. Teugels, and D.F.E. Thys Van Den Audenaerde. 1987. Revision de quelques *Barbus* à trois taches (Pisces, Cyprinidae) d'Afrique de l'Ouest avec la description de trois espèces nouvelles: *B. tiekoro* n. sp., *B. traorei* n. sp. et *B. trispiloides* n. sp. *Revue d'Hydrobiologie Tropicale* 20: 165–184.
- Lowenstein, J.H., T.W. Osmundson, S. Becker, R. Hanner, and M.L.J. Stiassny. 2010. Incorporating DNA barcodes into a multi-year inventory of the fishes of the hyperdiverse lower Congo River, with a multi-gene performance assessment of the genus *Labeo* as a case study. *Mitochondrial DNA* 21 (S2): 1–19.
- Mamonekene, V., and M.L.J. Stiassny. 2012a. A new *Bathyaethiops* (Characiformes: Alestidae) from the Lékoumou River (Kouilou-Niari Basin) in the Republic of Congo: first record of the genus in the lower Guinean ichthyofaunal province. *Copeia* 3: 478–483.
- Mamonekene, V., and M.L.J. Stiassny. 2012b. Fishes of the Du Chaillu Massif, Niari Depression, and Mayombe Massif (Republic of Congo, west-central Africa): A list of species collected in tributaries of the upper Ogowe and middle and upper Kouilou-Niari River basins. *Check List* 8 (6): 1172–1183.
- Monsembula Iyaba, R.J.C., and M.L.J. Stiassny. 2013. Fishes of the Salonga National Park (Congo basin, central Africa): a list of species collected in the Luilaka, Salonga, and Yenge Rivers (Equateur Province, Democratic Republic of Congo).

- Monsembula Iyaba, R.J.C., T. Liyandja, and M.L.J. Stiassny. 2013. Fishes of the N'sele River (Pool Malebo, Congo basin, Central Africa): a list of species collected in the main channel and affluent tributaries, Kinshasa Province, Democratic Republic of Congo. *Check List* 9 (5): 941–956.
- Paugy, D., C. Lévêque, and G.G. Teugels. 2003. Faune des poissons d'eaux douces et saumâtres de l'Afrique de l'Ouest. The fresh and brackish water fishes of West Africa, vol. 1. Paris: IRD Éditions, 457 pp.
- Poll, M. 1967. Contribution à la faune ichthyologique de l'Angola. *Diamang Publicações Culturais* 75. Lisbon: Dundo-Lunda/Museu do Dundo, 381 pp.
- Ren, Q., and R.L. Mayden. 2016. Molecular phylogeny and biogeography of African diploid barbs, '*Barbus*', and allies in Africa and Asia (Teleostei: Cypriniformes). *Zoologica Scripta* 45: 642–649.
- Sabaj, M.H. 2016. Standard symbolic codes for institutional resource collections in herpetology and ichthyology: an online reference. Version 6.5 (16 August 2016). Online resource (<http://www.asih.org>). Washington, D.C.: American Society of Ichthyologists and Herpetologists.
- Schmidt, R.C., and H.L. Bart. 2015. Nomenclatural changes should not be based on equivocally supported phylogenies: reply to Yang et al. 2015. *Molecular Phylogenetics and Evolution* 90: 193–194.
- Schneider, C.A., W.S. Rasband, and K.W. Eliceiri. 2012. NIH Image to ImageJ: 25 years of image analysis. *Nature Methods* 9: 671–675.
- Skelton, P.H. 2001. A complete guide to the freshwater fishes of southern Africa. Cape Town, South Africa: Struik Publishers, 395 pp.
- Skelton, P.H. 2016. Name changes and additions to the southern African freshwater fish fauna. *African Journal of Aquatic Sciences* 2016: 345–351.
- Stiassny, M.L.J., and H. Sakharova. 2016. Review of the smiliogastrin cyprinids of the Kwilu River (Kasai Basin, central Africa), revised diagnosis for *Clypeobarbus* (Cyprinidae: Cyprininae: Smiliogastrini) and description of a new species. *Journal of Fish Biology* 88 (4): 1394–1412.
- Stiassny, M.L.J., G.G. Teugels, and C.D. Hopkins. 2007. Poissons d'eaux douces et saumâtres de basse Guinée, ouest de l'Afrique centrale. The fresh and brackish water fishes of lower Guinea, west-central Africa, vol. 1. Paris: IRD Éditions, 800 pp.
- Stiassny, M.L.J., T.L.D. Liyandja, and R.J.C. Monsembula Iyaba. 2016. A new small barb (Cyprininae: Smiliogastrini) from the N'sele and Mayi Ndombe rivers in the lower reaches of the middle Congo basin (Democratic Republic of Congo, Central Africa). *American Museum Novitates* 3848: 1–15.
- Van Ginneken, M., E. Decru, E. Verheyen, and J. Snoeks. 2017. Morphometry and DNA barcoding reveal cryptic diversity in the genus *Enteromius* (Cypriniformes: Cyprinidae) from the Congo basin, Africa. *European Journal of Taxonomy* 310: 1–32.
- Walsh, G., M.N. Jonker, and V. Mamonekene. 2014. A collection of fishes from tributaries of the lower Kouilou, Noumbi and smaller coastal basin systems, Republic of Congo, Lower Guinea, west-central Africa. *Check List* 10 (4): 900–912.
- Yang, L., et al. 2015. Phylogeny and polyploidy: Resolving the classification of cyprinine fishes (Teleostei: Cypriniformes). *Molecular Phylogenetics and Evolution* 85: 97–116.