

Two new *Phenacogrammus* (Characoidei; Alestidae) from the Ndzaa River (Mfimi-Lukenie basin) of central Africa, Democratic Republic of Congo

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ABSTRACT

Two new *Phenacogrammus* are described from the Ndzaa River, a small left-bank tributary of the Mfimi-Lukenie River in the central Congo basin. They share with *P. deheyeni*, a congener endemic to the Cuvette Centrale to the north, a prominent anterior expansion of the first pleural rib; a feature interpreted here as a synapomorphy diagnostic for this species assemblage. The two new species are readily differentiated from *P. deheyeni* based on differences in pigmentation patterning, a lower number of scales in longitudinal series (26–28 vs. 29–33) and a longer head length (m. 24.9% SL vs. 21.7 and 23.2% SL). *Phenacogrammus flexus*, new species, is distinguished from all congeners in the possession of 6 (vs. 7) supraneural bones, and a characteristic zigzag pattern of black pigmentation along and below the midline extending from the posterior border of the opercle to the base of the caudal peduncle. While no unambiguous morphological autapomorphies have been located to diagnose *P. concolor*, new species, it is nonetheless readily distinguished from all congeners, except *P. deheyeni* and *P. flexus*, in the possession of a prominent anterior expansion of the first pleural rib. It differs from both *P. deheyeni* and *P. flexus* in the absence of a dominant pigmentation patterning over the flanks and caudal peduncle. Additionally, it differs from *P. flexus* in a shallower body depth (m. 24.9% vs. 27.0% SL) and in the possession of 7 (vs. 6) supraneurals.

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The three species exhibit extensive divergence in mt-COI sequence (*P. flexus* vs. *P. concolor* 10.2%–11%; *P. flexus* vs. *deheyni* 12.9%–13.5%; *P. concolor* vs. *deheyni* 11.3%–12.9%). Furthermore, analysis of shape variation utilizing geometric morphometrics indicates that each species differs significantly in body shape.

INTRODUCTION

During a survey of the fishes of the Mfimi River basin in central Congo, collections were made in the Ndzaa River, a small left-bank tributary entering the Mfimi near the settlement of Kutu at the outflow of Lake Mai-Ndombe, upstream of which the river is renamed the Lukenie (fig. 1). The Ndzaa (the Ndjua River on some maps) is a clear water stream meandering through dense riparian forest surrounded by open grasslands and savannah (fig. 2). Collections were made in July 2018, at the height of the main dry season in a short stretch of the river at about 25 km upstream of its junction with the Mfimi-Lukenie (fig. 1). In addition to samples of 27 species (table 1), seven of which had not previously been collected within the Mfimi basin (Stiassny et al., personal obs.) were specimens of two putatively undescribed alestid species belonging to the genus *Phenacogrammus* Eigenmann, 1907. Although the generic-level taxonomy of the Alestidae is generally poorly supported by apomorphy-based diagnoses (Stiassny and Schaefer, 2005; Schaefer, 2007; Arroyave and Stiassny, 2011) *Phenacogrammus* is currently diagnosed by the derived (reductive) feature of a truncated lateral line consisting of fewer pored than nonpored scales. While a truncated lateral line occurs in several other alestid taxa (Zanata and Vari, 2005) this feature, in combination with the presence of two small, usually conical, symphyseal teeth located immediately behind the multicuspidate outer row series on the dentary, serves to differentiate members of this genus from all others. Although taxon sampling within *Phenacogrammus* and across the family was incomplete, the molecular study of Arroyave and Stiassny (2011) provides support for the monophyly of *Phenacogrammus* as currently constituted (Fricke et al., 2021). Despite the shortcomings in our understanding of alestid generic composition and intrarelationships, an accurate accounting of species diversity is of central importance for phylogenetic resolution and for data-based conservation efforts (Stiassny and Mamonekene, 2007). And, as such, species discovery and description remain fundamental tasks for advancing biodiversity studies in poorly documented regions such as the central Congo basin where considerable phylogenetic diversity remains to be documented (Stiassny et al., 2011). While recognizing that future generic reassignment may be necessary, as a comparative framework for their diagnosis and description, we follow the differential generic diagnosis of *Phenacogrammus* provided by Poll (1967) and Zanata and Vari (2005) and assign the two new taxa from the Ndzaa River to this genus.

Prior to the present study, four species of *Phenacogrammus* had been reported from the central Congo basin: *P. polli*, *P. dehenyi*, *P. aurantiacus*, and *P. interruptus* (fig. 3A–D). The latter two species are reported to be widely distributed throughout the Congo basin; however, while *P. interruptus* appears to represent a single species across its extensive range, geo-

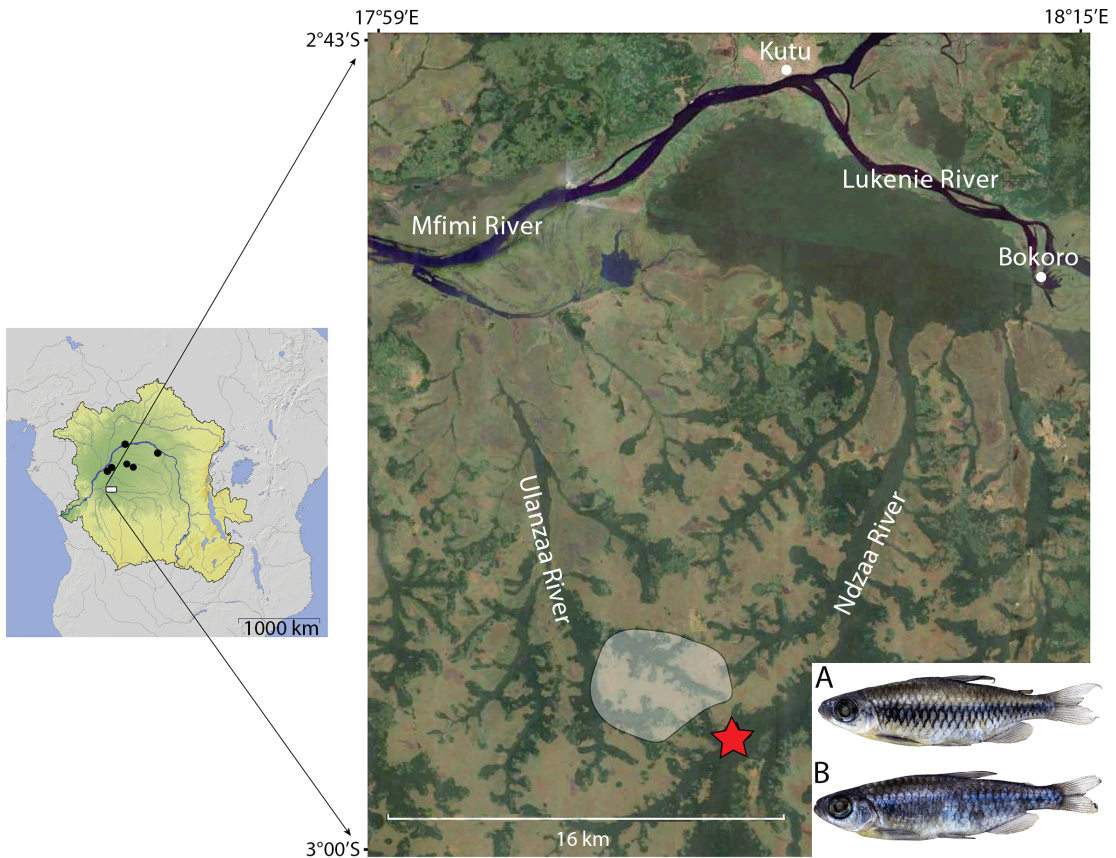


FIGURE 1. Left, location of study area in Congo basin (black circles indicate known range of *P. deheyeni*). Right, map of Mfimi-Lukenie region and location of Ndzaa River. Red star indicates region where collections were made. Shaded area in the Ulanzaa River catchment indicates the predicted region of highest habitat suitability based on preliminary species distribution modelling. Inset: A. *Phenacogrammus flexus*, B. *Phenacogrammus concolor*, shortly postmortem.

graphically disparate populations of *P. aurantiacus* exhibit morphological and coloration variation (data not shown) as well as considerable divergence in COI sequences (e.g., table 2), and likely represent multiple cryptic species. The other two species, *P. deheyeni* and *P. polli*, are currently known only from a few localities in the Cuvette Centrale, located to the north of the Mfimi-Lukenie basin (Poll, 1967; Monsembula Iyaba and Stiassny, 2013.). Based on a review of morphological features among *Phenacogrammus* and allied genera (Zanata and Vari, 2005; Arroyave and Stiassny, 2011) we note that the two Ndzaa species uniquely share with *P. deheyeni* (fig. 3B) a derived expansion of the first pleural rib, absent in all congeners and comparative material examined. The expansion of the first pleural rib is a feature interpreted here as a synapomorphy diagnostic for this species assemblage. Based on examination of these and additional comparative materials, we provide formal taxonomic descriptions of the two undescribed Ndzaa *Phenacogrammus*.



FIGURE 2. Upper panel shows a fisherman pointing to the type locality in the Ndzaa River where both new *Phenacogrammus* species were collected, and lower panel shows savannah/grassland surrounding the riparian cover of the river channel.

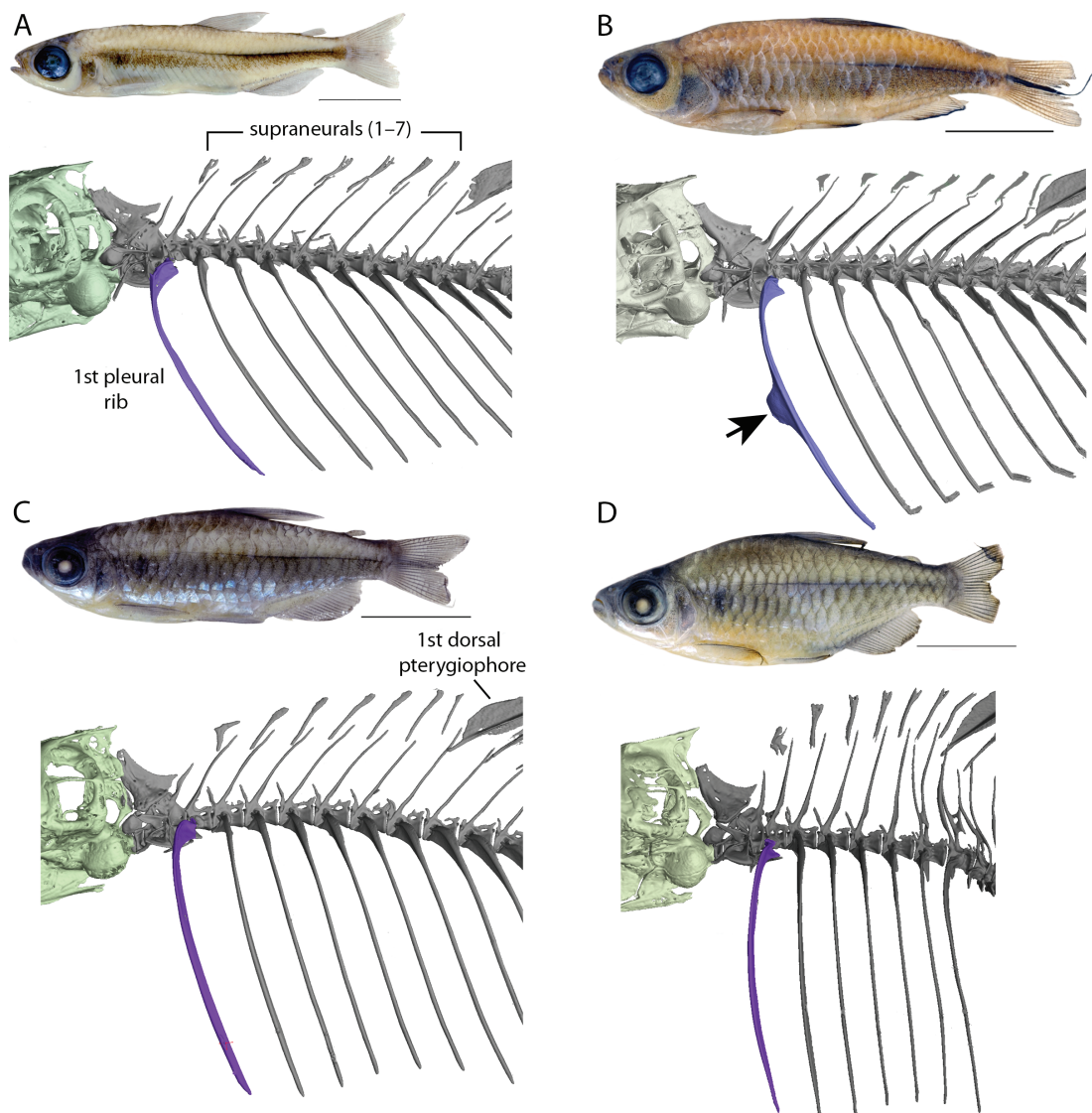


FIGURE 3. *Phenacogrammus* species previously reported from the central Congo basin (above) and posterior neurocranial and anterior axial anatomy rendered from μ CT scans (below). A. *P. polli*, B. *P. deheynei*, C. *P. aurantiacus*, and D. *P. interruptus*. Arrow indicates anterior expansion of the first pleural rib.

TABLE 1. List of species collected in the Ndzaa River. Taxa in bold type were not collected elsewhere within the Mfimi basin.

POLYPTERIFORMES
Polypteridae
<i>Polypterus retropinnis</i> Vaillant, 1899
OSTEOGLOSSIFORMES
Pantodontidae
<i>Pantodon buchholzi</i> Peters, 1876
Notopteridae
<i>Papyrocranus congoensis</i> (Nichols and La Monte, 1932)
<i>Xenomystus nigri</i> (Günther, 1868)
Mormyridae
<i>Petrocephalus balayi</i> Sauvage, 1883
<i>Petrocephalus odzalaensis</i> Lavoué, Sullivan and Arnegard, 2010
GONORHYNCHIFORMES
Phractolaemidae
<i>Phractolaemus ansorgii</i> Boulenger, 1901
CYPRINIFORMES
Cyprinidae
<i>Enteromius cf. miolepis</i> (Boulenger, 1902)
CHARACIFORMES
Alestidae
<i>Alestopetersius hilgendorfi</i> (Boulenger, 1899)
<i>Phenacogrammus cf. aurantiacus</i> (Pellegrin, 1930)
<i>Phenacogrammus flexus</i> , new species
<i>Phenacogrammus concolor</i> , new species
SILURIFORMES
Clariidae
<i>Clariallabes centralis</i> (Poll and Lambert, 1958)
<i>Clarias angolensis</i> Steindachner 1866
<i>Clarias camerunensis</i> Lönnberg, 1895
<i>Clarias pachynema</i> Boulenger, 1903
Malapteruridae
<i>Malapterurus microstoma</i> Poll and Gosse, 1969
<i>Paradoxoglanis caudovittatus</i> Norris, 2002
Claroteidae
<i>Notoglanidium macrostoma</i> (Pellegrin, 1909)
Schilbeidae
<i>Pareutropius debauwi</i> (Boulenger, 1900)
<i>Schilbe yangambianus</i> (Poll, 1954)

TABLE 1 *continued*

SYNBRANCHIFORMES
Mastacembelidae
<i>Mastacembelus greshoffi</i> Boulenger, 1901
ANABANTIFORMES
Anabantidae
<i>Ctenopoma nigropannosum</i> Reichenow, 1875
<i>Microctenopoma ansorgii</i> (Boulenger, 1912)
<i>Microctenopoma fasciolatum</i> (Boulenger 1899)
CICHLIFORMES
Cichlidae
<i>Congochromis sabinae</i> (Lamboj, 2005)
<i>Hemichromis lifalili</i> Loisel 1979
CYPRINODONTIFORMES
Nothobranchiidae
<i>Epiplatys chevalieri</i> (Pellegrin, 1904)
<i>Epiplatys multifasciatus</i> (Boulenger, 1913)

MATERIALS AND METHODS

MORPHOLOGY: Fourteen standard morphometric and eight meristic counts follow Paugy et al. (2003). Linear measurements were taken by photographing the left side of each specimen in an Ortech Professional Photobox Plus (Model 1419) on a platform with a Nikon D200 camera with a 60 mm f/2.8 AFMicro-Nikkor lens, and a 1 cm scale. Specimens were pinned to mark fins and other homologous anatomical features prior to photographing, and images uploaded into tpsDIG2 (Rolf, 2017). Measurements are presented as percentages of standard length (SL) or head length (HL) rounded to the nearest 0.1 mm. To count vertebrae and fin rays and visualize other skeletal features, specimens were X-rayed, and some were CT-scanned or cleared and stained following a modified protocol based on Taylor and van Dyke (1985). Vertebral counts include the four modified Weberian centra but exclude the terminal, hypural-bearing centrum. Longitudinal scale counts terminate at the hypural fold and do not include the few scales on the base of the caudal fin.

GEOMETRIC MORPHOMETRICS: Nondistorted specimens of *P. flexus* new species (n = 8), *P. concolor* new species (n = 5), and *P. deheyeni* (n = 11) were selected for geometric morphometric analysis. The *P. deheyeni* sample included both adult and juvenile specimens whereas *P. flexus* and *P. concolor* were represented only by adults. Photographs were taken on the left side of each specimen as described above, and a set of 19 homologous landmarks was selected to capture overall body shape (fig. 4A). Photographs were uploaded into tpsDIG2 (Rohlf, 2017), and tpsUtil 1.70 (Rohlf, 2019) was used to generate x-y coordinate files used in downstream analyses. To remove most variation associated with size, rotate each individual to a common alignment, and generate a consensus shape by calculating the average shape of all specimens included in the analysis, a generalized Procrustes analysis (GPA) was performed in MorphoJ 1.06d

TABLE 2. Distance matrix indicating percent similarity in partial cytochrome *c* oxidase subunit I (COI) sequences for representative *Phenacogrammus* species and two related alestids (*Alestopterus nigropterus* and *Clupeocharax schoutedeni*). Comparison between individuals of the two new species, *P. flexus* and *P. concolor*, indicated in bold type.

tissue code	taxon	A.n	C.s	P.fl	P.f2	P.f3	P.f4	P.c1	P.c2	P.c3	P.c4	P.d1	P.d2	P.i1	P.i2	P.i3	P.i4	P.i5	P.i6	Pa1	Pa2	Pa3	Pa4	Pa5	Pt	Pu1	Pu2
AMCC 258388	<i>A. nigropterus</i> (A.n)																										
AMCC 258411	<i>C. schoutedeni</i> (C.s)	81.9																									
AMCC 258432	<i>P. flexus</i> (P.fl)	83.7	83.2																								
AMCC 258430	<i>P. flexus</i> (P.f2)	83.9	83.4	99.8																							
AMCC 258431	<i>P. flexus</i> (P.f3)	83.7	83.2	100	99.8																						
AMCC 258429	<i>P. flexus</i> (P.f4)	83.7	83.2	100	99.8	100																					
AMCC 258437	<i>P. concolor</i> (P.c1)	85.2	83.2	89.1	89.8	89.1	89.0																				
AMCC 258436	<i>P. concolor</i> (P.c2)	85.4	82.9	89.7	90.0	89.7	89.5	99.2																			
AMCC 258435	<i>P. concolor</i> (P.c3)	85.0	83.0	89.4	89.6	89.4	89.4	99.3	99.6																		
AMCC 258434	<i>P. concolor</i> (P.c4)	84.9	82.9	89.2	89.5	89.2	89.0	99.2	99.6	99.1																	
AMCC 197088	<i>P. deheyni</i> (P.d1)	84.2	82.4	86.5	87.1	86.5	87.1	87.1	87.7	88.7	87.9																
AMCC 209924	<i>P. deheyni</i> (P.d2)	84.2	82.4	86.5	87.1	86.5	87.1	87.1	87.7	88.7	87.9	100															
AMCC 258421	<i>P. interruptus</i> (P.i1)	83.9	83.4	87.3	87.6	87.3	87.1	87.1	87.7	88.2	87.3	91.3	91.3														
AMCC 258420	<i>P. interruptus</i> (P.i2)	83.7	83.2	86.6	87.3	86.6	86.6	86.6	87.1	87.4	86.6	90.7	90.7	99.0													
JFP 02-029	<i>P. interruptus</i> (P.i3)	83.7	82.7	87.7	88.1	87.7	87.6	87.5	88.1	88.7	87.7	91.9	91.9	99.0	98.3												
AMCC 263187	<i>P. interruptus</i> (P.i4)	83.7	82.7	87.7	88.1	87.7	87.6	87.5	88.1	88.7	87.7	91.9	91.9	99.0	98.3	100											
DRC-2009/0759	<i>P. interruptus</i> (P.i5)	83.2	82.2	87.9	88.3	87.9	87.8	87.7	88.3	88.9	87.9	91.9	91.9	98.6	97.8	99.6	99.6										
AMCC 116673	<i>P. interruptus</i> (P.i6)	83.4	82.4	87.9	88.3	87.9	87.8	87.7	88.3	88.9	87.9	92.1	92.1	98.8	98.1	99.8	99.8	99.8									
AMCC 258418	<i>P. aurantiacus</i> (Pa1)	84.4	81.7	86.9	87.1	86.9	87.1	86.7	87.3	88.7	87.7	99.0	99.0	91.3	90.7	91.9	91.9	92.1									
AMCC 258416	<i>P. aurantiacus</i> (Pa2)	84.2	81.5	86.5	86.9	86.5	86.8	86.7	87.3	88.4	87.7	99.0	99.0	90.9	90.4	91.5	91.5	91.7	99.6								
AMCC 205328	<i>P. aurantiacus</i> (Pa3)	84.9	85.1	89.5	88.6	89.5	88.0	90.1	90.7	90.8	90.7	88.5	88.5	88.9	87.8	88.5	88.5	88.7	88.7	88.3	87.9						
DRC-2009/0780	<i>P. aurantiacus</i> (Pa4)	84.7	83.9	88.5	88.3	88.5	87.8	90.3	90.9	91.3	90.9	88.1	88.1	89.9	88.8	89.3	89.3	89.5	89.5	88.3	87.9	97.0					
DRC-2009/0781	<i>P. aurantiacus</i> (Pa5)	84.4	83.4	88.3	87.8	88.3	87.3	90.1	90.7	90.8	90.5	87.7	87.7	89.1	88.0	88.9	88.9	89.1	89.1	87.9	87.5	96.8	99.2				
Cam-08/001	<i>P. taeniatus</i> (Pt)	88.2	82.7	84.2	84.6	84.2	83.8	84.6	85.4	86.1	84.9	85.8	86.7	86.1	86.5	86.5	86.7	86.7	85.8	85.4	85.2	84.4	84.2				
AMCC 227077	<i>P. urotaenia</i> (Pu1)	87.2	83.2	88.7	89.5	88.7	89.2	87.9	88.5	88.9	88.1	89.5	89.5	89.3	88.0	89.5	89.5	89.5	89.7	89.7	89.3	89.5	88.7	88.3	85.8		
AMCC 227078	<i>P. urotaenia</i> (Pu2)	87.2	83.2	88.7	89.5	88.7	89.2	87.9	88.5	88.9	88.1	89.5	89.5	89.3	88.0	89.5	89.5	89.5	89.7	89.7	89.3	89.5	88.7	88.3	85.8	100	
AMCC 205325	<i>P. urotaenia</i> (Pu3)	86.7	82.7	88.7	89.5	88.7	89.2	87.5	88.1	88.4	87.7	89.1	88.9	87.6	89.1	89.1	89.1	89.1	89.3	89.3	88.9	89.1	88.3	87.9	85.8	99.6	99.6

(Klingenberg, 2011). A covariate matrix was then constructed to prepare data for a principal component analysis (PCA), which was also conducted in MorphoJ. To investigate shape variation across the three species, a canonical variates analysis (CVA) incorporating a permutation test for pairwise differences with 10,000 iterations was conducted in MorphoJ (data not shown).

COI BARCODING: Total genomic DNA was extracted from available representatives of *Phenacogrammus* and from exemplars of two alestid genera (*Clupeocharax*, *Alestopetersius*) considered close relatives of *Phenacogrammus* (Zanata and Vari, 2005; Arroyave and Stiassny, 2011). Amplification and sequencing of partial cytochrome *c* oxidase subunit I (COI) was carried out as described in Stiassny and Alter (2015). We used Geneious Prime 2021.1.1 to manually edit and align sequences and to generate a distance matrix indicating the percentage identity (% of bases that are identical) in COI sequences between sampled taxa (table 2). Specimen catalog numbers, tissue codes, locality information, and GenBank accession numbers for sequences utilized in this study are provided in table 3.

ABBREVIATIONS: AMCC, Ambrose Monell Cryo Collection of the American Museum of Natural History; C&S, cleared and stained specimens; CT, micro-CT scanned specimens, SL, standard length; HL, head length; m, mean. Institutional abbreviations follow Sabaj (2016).

MORPHOMETRIC RESULTS

The first four principal components combined describe 72.7% of shape variation across the three species (fig. 4B). PC 1 accounts for 26.6% of total variation and reflects the considerable size variation between sampled specimens of *P. deheynei* vs. that of the two new species. Best separation among the three was obtained plotting PC2 (20.2%), which mainly describes variation in head size, against PC3 (14.9%) mainly describing variation in body depth (fig. 4B). Permutation test for Procrustes (p-value <0.005) and Mahalanobis distances (p-value <0.001) indicate that the three species are significantly different in body shape. Both the PC and CV analyses confirm that *P. deheynei* can be distinguished from both *P. flexus* and *P. concolor* in possessing a longer head, whereas *P. flexus* can be distinguished from *P. concolor* by a deeper body.

COI BARCODING RESULTS

The mitochondrial cytochrome *c* oxidase I gene (COI) has long been used to detect both described and undescribed fish species (e.g., Hubert et al., 2008; Ward, 2009; Decru et al., 2016), and the COI distance matrix (table 2) provides additional support for the current hypothesis of species identity for *P. flexus* and *P. concolor* as distinct from *P. deheynei* and other congeners. The percentage divergence in mt-COI sequence among individuals of *P. flexus* is 0%–0.2%, and of *P. concolor* is 0.6%–0.9%. In contrast sequence divergence between individuals of *P. flexus* and *P. concolor* is 10.2%–11% (bold font in table 2), between *P. flexus* and *P. deheynei* is 12.9%–13.5%, and between *P. concolor* and *P. deheynei* is 11.3%–12.9%, each of which far exceeds the traditionally employed ca. 3% sequence divergence heuristic threshold for conspecifics (Avise, 2000; Hebert et al., 2003, 2004; Arroyave et al., 2019).

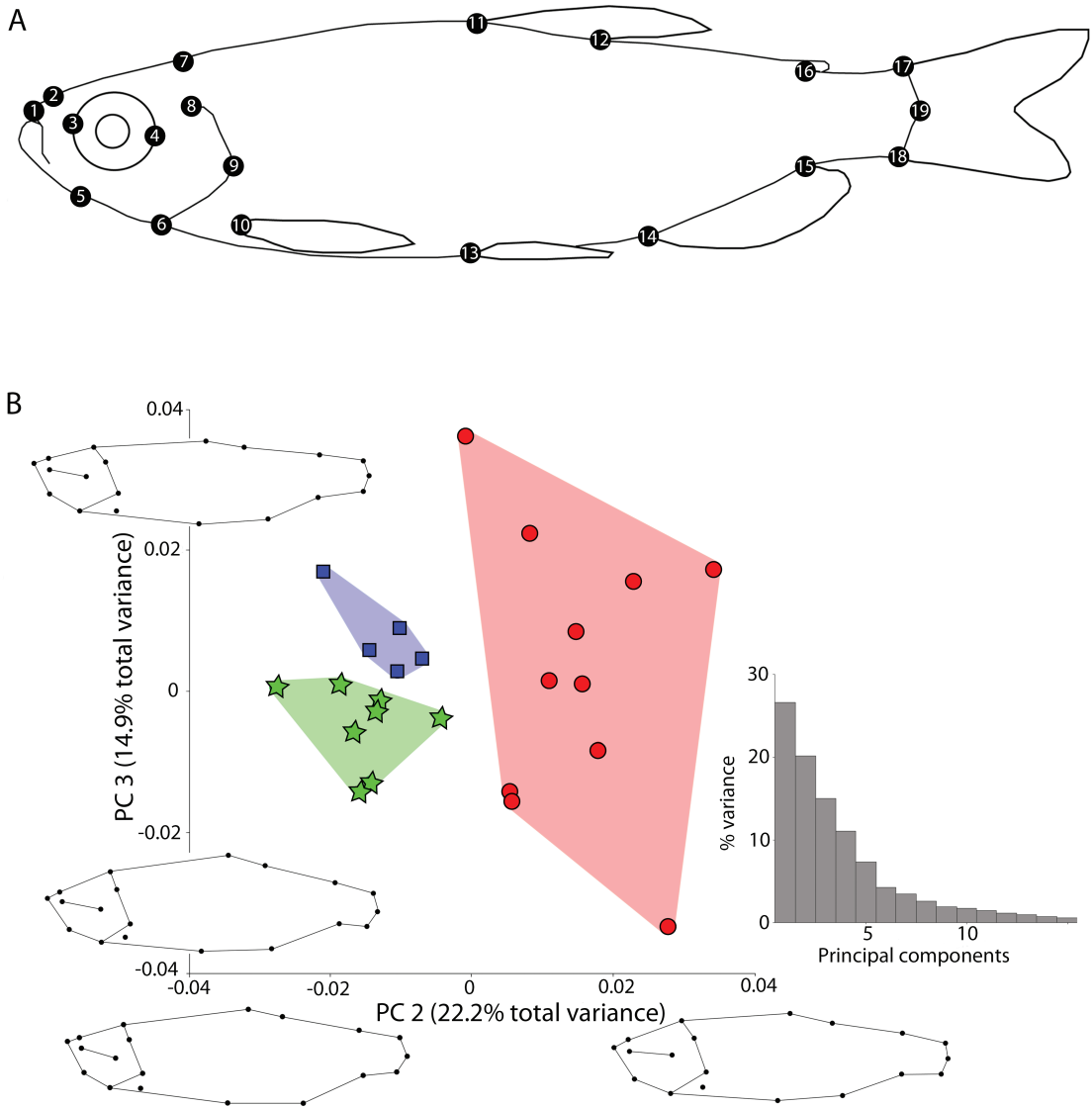


FIGURE 4. **A.** outline showing locations of 19 homologous landmarks selected to capture overall body shape. **B.** Principal components analysis of body shape with deformations as implied by PC2 and PC3 scores using Procrustes superposition of the 19 landmarks. Inset: plot of % variance explained by each PC. Stars, *P. flexus* new species; squares, *P. concolor* new species; circles, *P. deheyeni*.

Phenacogrammus flexus, new species

Figures 1, 5; table 4

HOLOTYPE: AMNH 274785, 47.2 mm SL, Democratic Republic of Congo, Mai-Ndombe Province, Ndzaa River (02° 58' 25.0"S 018° 7' 55.26"E), R. Monsembula Iyaba et al., 25 July 2018.

PARATYPES: AMNH 276320, 7 specimens, 2 CT-scanned, 47.0–37.8 mm SL, same data as holotype.

DIAGNOSIS: Distinguished from all congeners except *P. deheyni* and *P. concolor* by the presence of a prominent anterior expansion of the first pleural rib. Further distinguished from all congeners in the possession of 6 (vs. 7) supraneural bones, and a characteristic zigzag pattern of black pigmentation along and below the midline extending from the posterior border of the opercle to the base of the caudal peduncle.

DESCRIPTION: Based on the holotype and seven paratypes. General appearance as in figure 5A; proportional measurements and meristic counts are given in table 4. A small-bodied species, maximum observed size 47.2 mm SL. Body relatively elongate, somewhat laterally compressed with greatest body depth (m. 27.0% SL) a little in front of dorsal-fin origin at level of pelvic-fin insertion. Dorsal body profile steeply convex to dorsal fin, slightly less so to caudal-fin base. Ventral profile smoothly convex between isthmus and anal-fin base, caudal peduncle longer than deep. Head length short (m. 23.4% SL), eye large, bony orbit diameter m. 43.9% HL.

Mouth terminal, lower jaw prominent and slightly prognathous, lower lip thick. Premaxilla with two teeth in outer row, each bearing 3 cusps, positioned opposite interspaces between and alternating with 4 inner row teeth bearing 4–5 cusps. Four outer row teeth on each dentary, the first 3 bearing 5 cusps, and the 4th greatly reduced in size bearing 3 cusps. Two small, conical, symphyseal teeth located immediately behind outer row series on dentary (fig. 5C). Dorsal-fin rays ii.7–8, fin positioned midway between snout and caudal-fin base, origin at, or slightly behind, pelvic-fin insertion, first two branched rays somewhat elongated but not filamentous. Anal fin iii.17–18 rays, no hypertrophy or posterior curvature of anal fin in males. Caudal fin forked, with 8 upper and 9 lower principal rays, no median filamentous extension. Scales in longitudinal series 26–27 (mode 26) to caudal flexure, 4–5 transverse scales between longitudinal series and dorsal-fin origin, 3 transverse scales between longitudinal series and pelvic-fin insertion. Pored scales in truncate lateral line 7–8 (mode 8). Circumpeduncular scales 10. Vertebral count 31–32. Twelve to 13 pleural ribs, first with prominent rounded expansion on anterior face in upper third (fig. 5B). Six tubular supraneurals located between interspaces of neural spines of vertebral centra 4–10.

COLORATION: In preservation (fig. 5A), base body coloration yellowish, darker dorsally and with an overlay of silver iridescence ventrally along flanks. Snout and dorsum of head dark brownish black, cheek silver with patches of melanophores. A prominent pattern of black pigmentation encircling scales of longitudinal series along and below midline extending from posterior border of opercle to base of caudal fin, becoming broken into a zigzag band posteriorly along flanks and caudal peduncle. No trace of a humeral blotch. Dorsal and adipose fin grayish black, anal fin dusky, pectoral and pelvic fins hyaline with darkly pigmented leading edges. Median rays of caudal fin somewhat darker than above and below. Coloration and pigmentation shortly postmortem (fig. 1A) like that in preservation, but generally more intense.

DISTRIBUTION: Currently known only from the type locality, a shallow pool like expansion of the Ndzaa River (fig. 2, upper panel), about 25 km upstream of the outflow of the Ndzaa into the Mfimi (fig. 1).

TABLE 3. Specimen catalog numbers, tissue codes, locality information, and GenBank accession numbers for COI sequences utilized in this study. Democratic Republic of Congo, D.R.C.

Taxon	Catalog number	Tissue code	Locality	coordinates	COI
<i>Alestopetersius nigropterus</i>	AMNH 274754	AMCC 258388	Nioki Port Market, Mfimi River, Mai-Ndombe Province, D.R.C.	02 43 25.4S 17 41 38.5E	OK396005
<i>Clupeocharax schoutedeni</i>	AMNH 274775	AMCC 258411	Lomomo River near confluence with Mfimi, Mai-Ndombe Province, D.R.C.	02 45 19.74S 17 55 55.80E	OK396004
<i>Phenacogrammus flexus</i> , n. sp.	AMNH 274785	AMCC 258429	Ndzaa River near Mushimine Village, Mai-Ndombe Province, D.R.C.	02 58 25.08S 18 07 55.26E	OK396008
<i>Phenacogrammus flexus</i> , n. sp.	AMNH 276320	AMCC 258430	Ndzaa River near Mushimine Village, Mai-Ndombe Province, D.R.C.	02 58 25.08S 18 07 55.26E	OK396011
<i>Phenacogrammus flexus</i> , n. sp.	AMNH 276320	AMCC 258431	Ndzaa River near Mushimine Village, Mai-Ndombe Province, D.R.C.	02 58 25.08S 18 07 55.26E	OK396009
<i>Phenacogrammus flexus</i> , n. sp.	AMNH 276320	AMCC 258432	Ndzaa River near Mushimine Village, Mai-Ndombe Province, D.R.C.	02 58 25.08S 18 07 55.26E	OK396010
<i>Phenacogrammus concolor</i> , n.sp.	AMNH 276321	AMCC 258434	Ndzaa River near Mushimine Village, Mai-Ndombe Province, D.R.C.	02 58 25.08S 18 07 55.26E	OK396012
<i>Phenacogrammus concolor</i> , n. sp.	AMNH 276321	AMCC 258435	Ndzaa River near Mushimine Village, Mai-Ndombe Province, D.R.C.	02 58 25.08S 18 07 55.26E	OK396015
<i>Phenacogrammus concolor</i> , n. sp.	AMNH 276321	AMCC 258436	Ndzaa River near Mushimine Village, Mai-Ndombe Province, D.R.C.	02 58 25.08S 18 07 55.26E	OK396014
<i>Phenacogrammus concolor</i> , n. sp.	AMNH 276321	AMCC 258437	Ndzaa River near Mushimine Village, Mai-Ndombe Province, D.R.C.	02 58 25.08S 18 07 55.26E	OK396013
<i>Phenacogrammus deheyeni</i>	AMNH 252194	AMCC 197088	River Ta'Simon at Boaugi, Tshuapa Province, D.R.C.	01 59 21.3S 20 58 17.0E	OK396006
<i>Phenacogrammus deheyeni</i>	AMNH 252251	AMCC 209924	Bosombangwa, Salonga National Park, Tshuapa Province, D.R.C.	02 08 20.66S 21 06 51.23E	OK396007

TABLE 3 continued

Taxon	Catalog number	Tissue code	Locality	coordinates	COI
<i>Phenacogrammus interruptus</i>	AMNH 274781	AMCC 258420	Mfimi main channel at Nioki Port, Mai-Ndombe Province, D.R.C.	02 43 25.4S 17 41 38.5E	OK562204
<i>Phenacogrammus interruptus</i>	AMNH 274782	AMCC 258421	Mfimi at confluence with Ndombolo River, Mai-Ndombe Province, D.R.C.	02 47 26.30S 17 44 49.45E	OK562196
<i>Phenacogrammus interruptus</i>	CU 89868	JFP 02-029	Lekoli River, Odzala National Park, Cuvette Ouest, Republic of Congo	00 37 12.00N 14 55 5.98E	OK562206
<i>Phenacogrammus interruptus</i>	AMNH 247289	AMMC 263187	Rocks below CO8-028 near Bulu, Kongo Central Province, D.R.C.	5 02 52.31S 13 59 49.18E	OK562207
<i>Phenacogrammus interruptus</i>	ZSM 39401	DRC-2009/0759	Ikonga stream at mouth in Yaekama, Tshopo Province, D.R.C.		JF800977
<i>Phenacogrammus interruptus</i>	AMNH 233442	AMCC 116673	Aquarium import, no locality data		OK562208
<i>Phenacogrammus aurantiacus</i>	AMNH 274780	AMCC 258418	Ndzaa River near Mushimine Village, Mai-Ndombe Province, D.R.C.	02 58 25.08S 18 07 55.26E	OK562202
<i>Phenacogrammus aurantiacus</i>	AMNH 274779	AMCC 258416	Mfimi main channel at Nioki Port, Mai-Ndombe Province, D.R.C.	02 43 25.4S 17 41 38.5E	OK562203
<i>Phenacogrammus aurantiacus</i>	AMNH 262366	AMCC 205328	WCTS Forestry Concession, Site 2, Ogowe-Ivindo, Gabon	00 25 24.20N 12 53 22.27E	OK562197
<i>Phenacogrammus aurantiacus</i>	ZSM 39495	DRC-2009/0780	Bakere River at Yambula-Bakere, Bas-Uele Province, D.R.C.		OK562198
<i>Phenacogrammus aurantiacus</i>	ZSM 39495	DRC-2009/0781	Bakere River at Yambula-Bakere, Bas-Uele Province, D.R.C.		OK562199
<i>Phenacogrammus taeniatus</i>	ZSM 36901	Cam-08/001	Sangha River at Libongo, Southeast Province, Cameroon		OK562195
<i>Phenacogrammus urotaenia</i>	AMNH 262979	AMCC 227077	Affluent of Gniabale upstream of confluence with Ivindo, Gabon	00 27 12.80N 12 46 03.11E	OK562200
<i>Phenacogrammus urotaenia</i>	AMNH 262979	AMCC 227078	Affluent of Gniabale upstream of confluence with Ivindo, Gabon	00 27 12.80N 12 46 03.11E	OK562201
<i>Phenacogrammus urotaenia</i>	AMNH 262365	AMCC 205325	WCTS Forestry Concession, Site 2, Ogowe-Ivindo, Gabon	00 25 24.20N 12 53 22.27E	JF800974

ETYMOLOGY: *Flexus*, from the Latin, meaning winding, zigzag, or sharp turn. Named in reference to the prominent pattern of black pigmentation along the flanks and caudal peduncle.

Phenacogrammus concolor, new species

Figures 1, 6; table 5

HOLOTYPE: AMNH 274786, 43.9 mm SL, Democratic Republic of Congo, Mai-Ndombe Province, Ndzaa River (02° 58' 25.0"S 018° 7' 55.26"E), R. Monsembula Iyaba et al., 25 July 2018.

PARATYPES: AMNH 276321, 4 specimens, 2 CT-scanned, 42.9–34.5 mm SL, same data as holotype.

DIFFERENTIAL DIAGNOSIS: While no unambiguous morphological autapomorphies have been located to diagnose *P. concolor* the species is nonetheless distinguished from all congeners except *P. deheyeni* and *P. flexus* in the possession of a prominent anterior expansion of the first pleural rib. The species is readily differentiated from both in the absence of a dominant pigmentation patterning over the flanks and caudal peduncle. Additionally, it differs from *P. flexus* in a shallower body depth (m. 24.9% vs. 27.0% SL), and in the possession of 7 (vs. 6) supraneurals.

DESCRIPTION: Based on the holotype and four paratypes. General appearance as in figure 6A, proportional measurements and meristic counts are given in table 5. A small-bodied species, maximum observed size 43.9 mm SL. Body elongate, laterally compressed with greatest body depth (m. 24.9% SL) well in front of dorsal-fin origin, in front of the level of pelvic-fin insertion. Dorsal body profile smoothly convex to dorsal fin, slightly less so to caudal-fin base. Ventral profile smoothly convex between isthmus and anal-fin base, caudal peduncle longer than deep. Head length short (m. 21.7% SL), eye large, bony orbit diameter m. 44.8% HL.

Mouth terminal, lower jaw prominent and slightly prognathous, lower lip thick. Premaxilla with two teeth in outer row, each bearing 3 cusps, positioned opposite interspaces between and alternating with 4 inner row teeth bearing 5–6 cusps. Four robust, broad-based, outer-row teeth on each dentary, first 3 bearing 5–6 cusps, and 4th greatly reduced in size bearing 3 cusps. Two small, conical, symphyseal teeth located immediately behind outer row series on dentary (fig. 6C). Dorsal-fin rays ii.7–8, fin positioned midway between snout and caudal-fin base, with origin at, or slightly in front of, pelvic-fin insertion, first two branched rays not elongated. Anal fin iii.15–16 rays, no hypertrophy or posterior curvature of anal fin in males. Caudal fin forked, with 9 upper and 9 lower principal rays, no median filamentous extension. Scales in longitudinal series 26–28 (mode 28) to caudal flexure, 3 or 4 transverse scales between longitudinal series and dorsal-fin origin, 3 transverse scales between longitudinal series and pelvic-fin insertion. Pored scales in truncate lateral line 5–7 (mode 6). Circumpeduncular scales 10. Vertebral count 31–33. Twelve–13 pleural ribs, first with prominent rounded expansion on anterior face in upper third (fig. 5B). Seven tubular supraneurals located between interspaces of neural spines of vertebral centra 4–11.

COLORATION: In preservation (fig. 6A), base body coloration grayish brown, darker dorsally and becoming pale yellow on chest and ventrum. An overlay of bluish iridescence covers most of body. Snout and dorsum of head dark brownish black, cheek silver with a few scattered mela-

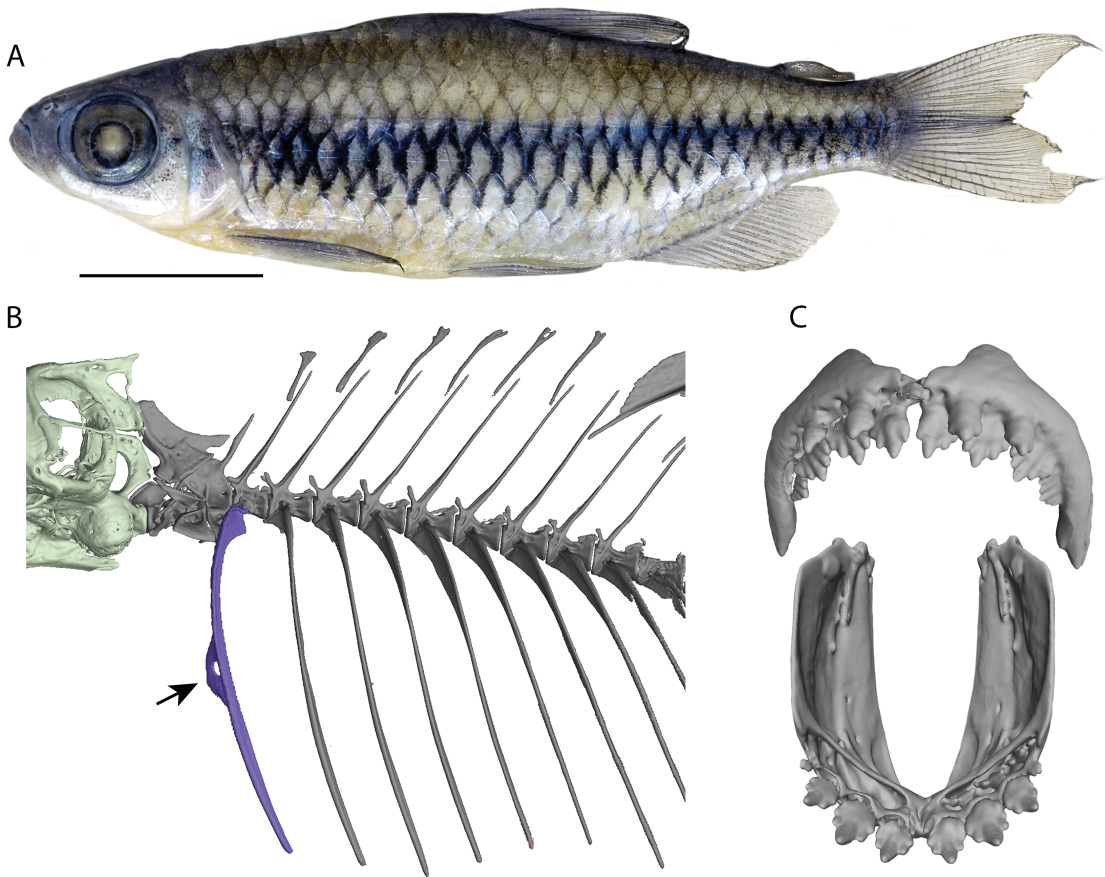


FIGURE 5. **A.** *Phenacogrammus flexus*, new species (holotype, AMNH 274785). **B.** Posterior neurocranial and anterior axial anatomy rendered from μ CT scans; arrow indicates location of anterior expansion of the first pleural rib. **C.** Premaxillary and dentary tooth insertion and cuspidation rendered from μ CT scan.

nophores. A large humeral blotch present at midbody, above pectoral fin. Other than humeral blotch no prominent pigmentation along flanks or caudal peduncle. Dorsal and adipose fin light gray, anal fin dusky distally, pectoral and pelvic fins hyaline with darkly pigmented leading edges. Median rays of caudal fin somewhat darker than above and below. Coloration and pigmentation shortly postmortem (fig. 1B) like that in preservation, but more intense.

DISTRIBUTION: Currently known only from the type locality, a shallow pool like expansion of the Ndzaa River (fig. 2, upper panel), about 25 km upstream of the outflow of the Ndzaa into the Mfimi (fig. 1).

ETYMOLOGY: *Concolor*, from the Latin, meaning of the same, or uniform, color. Named in reference to the absence of prominent pattern of black pigmentation along the flanks and caudal peduncle.

COMPARATIVE MATERIALS EXAMINED: *Alestopetersius hilgendorffii*: AMNH 244114, 5 specimens, 1CT, 1C&S, Democratic Republic of Congo, Salonga National Park, Yenge River at Boyenga. – MRAC 829, lectotype, Kutu. – *Alestopetersius brichardi*: AMNH 240416, 5 specimens,

TABLE 4. Morphometric measurements and meristic data for the holotype and seven paratypes of *Phenacogrammus flexus*, new species. Mean values include measurements of the holotype.

Morphometric measurements	Holotype	Paratypes		
		mean	max	min
Standard length (mm)	47.2		46.8	37.8
% SL				
Body depth	28.5	27	28.5	25.5
Head length	22.3	23.2	25	22.3
Dorsal-fin base	9.6	11.1	12.6	9.7
Anal-fin base	19.1	19.7	21.8	18.4
Predorsal length	53.9	52.9	55.1	49.8
Preanal length	69.5	69.6	71.4	67.9
Prepelvic length	48.9	49.2	51	47.9
Caudal peduncle length	17.1	16.4	18.7	14.9
Caudal peduncle depth	10.3	10.1	10.8	8.5
% HL				
Eye diameter (bony orbit)	46.1	43.9	46.1	39.8
Upper jaw length	44.2	41.4	47.2	35.1
Lower jaw length	51.9	48.9	52.8	44.1
Snout length	28.8	28.5	31.9	21.6

Meristic counts	Holotype	mode	max	min
Total vertebral count	32	31	32	31
Dorsal-fin rays	ii8	ii8	ii8	ii7
Anal-fin rays	iii18	iii18	iii18	iii17
Pored lateral line scales	8	8	8	7
Longitudinal scales	26	26	27	26
Scales to dorsal-fin origin	5	5	5	4
Scales to pelvic-fin insertion	3	3	3	3
Circumpeduncular scale rows	10	10	10	10

1C&S, Republic of Congo, Cuvette Ouest, Odzala National Forest, au campement des pêcheurs. – MRAC 121105, holotype, Yangambi, Lac Yandja. – *Alestopetersius nigropterus*: AMNH 274754, 1 specimen, Democratic Republic of Congo, Mai-Ndombe Province, Nioki Port Market, main channel Mfimi River.

Nannopetersius ansorgii: AMNH 263093, 5 specimens, 1CT, Republic of Congo, Kouilou Province, Lake Tchibanji. – NHMUK 1910.11.28:71, lectotype, Angola, Bengo River at Cabiri and Lake Kilungu. – *Nannopetersius lamberti*: AMNH 253898, 5 specimens, 2C&S, Republic of Congo, Passi-passi River.

Clupeocharax schoutedeni: AMNH 274775, 1 specimen, Democratic Republic of Congo, Mai-Ndombe Province, Lomomo River near confluence with Mfimi.

Phenacogrammus aurantiacus: AMNH 274780, 3 specimens, 2CT, Democratic Republic of Congo, Mai-Ndombe Province, Ndzaa River. – AMNH 2474779, 3 specimens, Democratic Republic of Congo, Mai-Ndombe Province, Mfimi River around Nioki Port. – AMNH 260346, 5 specimens, Central African Republic, Dzanga-Sangha Protected Area. – AMNH 262366, 1 specimen, Gabon, Ogowe-Ivindo, WCTS Forestry Concession, Site 2. – AMNH 274861, 4 specimens, Republic of Congo, Kouyou River at Owando, 1 hour upstream from the bridge.

Phenacogrammus deheyni: 244045, 2 specimens, 1CT, Democratic Republic of Congo, Salonga National Park, Salonga River at Bokuma. – AMNH 244047, 1 specimen, 1CT, Democratic Republic of Congo, Salonga National Park, Yenge River at Boyenga. – AMNH 252208, 2 specimens, 1CT, Democratic Republic of Congo, Salonga National Park, Bionga Bionga. – MRAC 57789, holotype, Mumbia, Territory of Lisala. – AMNH 252277, 3 specimens, Democratic Republic of Congo, Mpongo stream ca. 2 km from Luilaka River. – AMNH 252194, 1 specimen, Democratic Republic of Congo, Ta'Simon River at Boaugi.

Phenacogrammus interruptus: AMNH 274784, 2 specimens, 2CT, Democratic Republic of Congo, Mai-Ndombe Province, Lomomo River near Kilako. – AMNH 256217, 3 specimens, 1C&S, Democratic Republic of Congo, Kwilu River at Kwilu beach. – AMNH 268936, 1 specimen, Democratic Republic of Congo, Kinshasa Province, Pool Malebo at Kinkole. – MRAC 817, lectotype, Stanley Pool. – CU 89868, 1 specimen, Republic of Congo, Lekoli River, Odzala National Park. – AMNH 247289, 1 specimen, Democratic Republic of Congo, Kongo Central Province, rocks below CO8-028 near Bulu. – AMNH 233442, 1 specimen, Aquarium purchase, no locality data.

Phenacogrammus major: AMNH 236514, 1 specimen, 1CT, Cameroon, Pont So'o at confluence of the So'o and Fala Rivers.

Phenacogrammus polli: AMNH 240816, 3 specimens, 2CT, Democratic Republic of Congo, Salonga National Park, Luilaka River at Nkombe-Dunda. – AMNH 273785, 4 specimens, Democratic Republic of Congo, Salonga National Park, Luilaka River at Ifumu. – AMNH 240793, 5 specimens, 2C&S, Democratic Republic of Congo, Salonga National Park, Luilaka River at Boangi Village. – MRAC 125500, holotype, River Lomela at Lomela.

Phenacogrammus taeniatus: ZSM 36901, Cameroon, Southeast Province, Sangha River at Libongo.

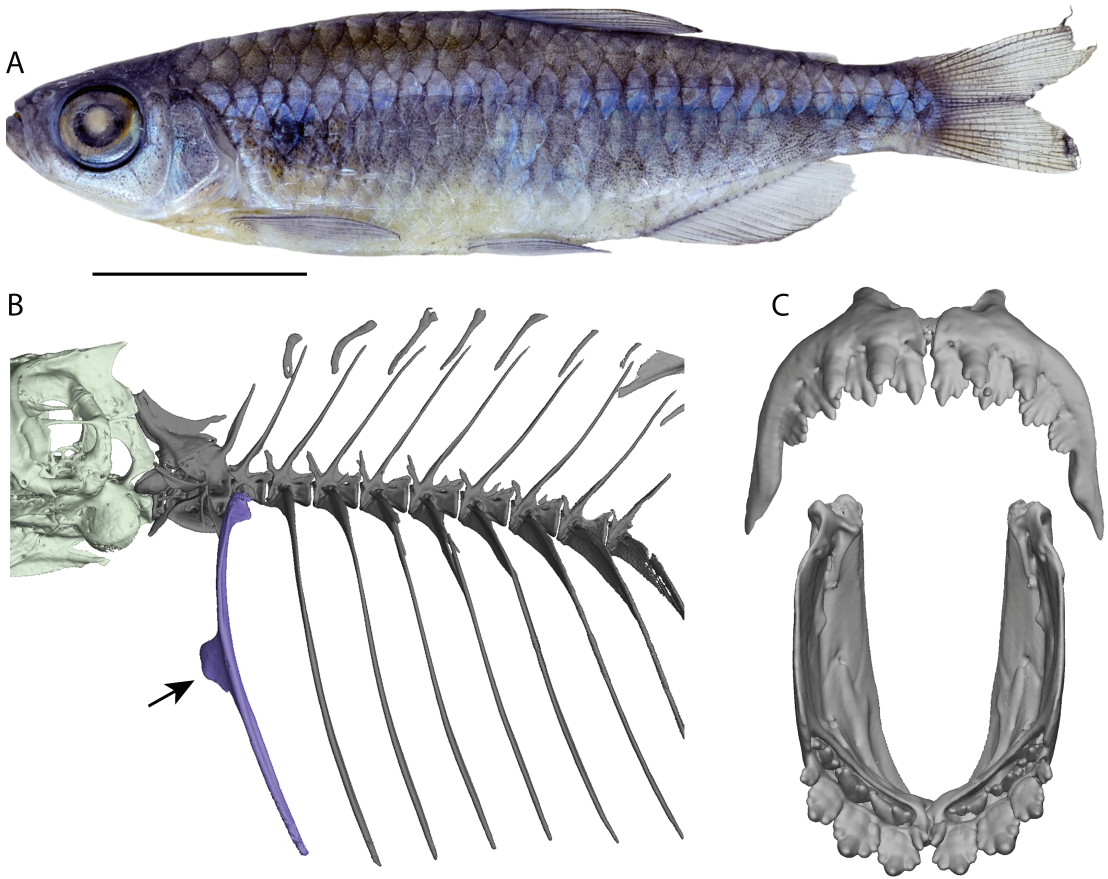


FIGURE 6. **A.** *Phenacogrammus concolor*, new species (holotype, AMNH 274786). **B.** Posterior neurocranial and anterior axial anatomy rendered from μ CT scans; arrow indicates location of anterior expansion of the first pleural rib. **C.** Premaxillary and dentary tooth insertion and cuspidation rendered from μ CT scan.

Phenacogrammus urotaenia: AMNH 253971, 5 specimens, 1CT, Republic of Congo, Kouilou Province, Lebayi River. – AMNH 262979, 5 specimens, 1C&S, Gabon, Ogowe-Ivindo, small affluent of the Gniabale River. – AMNH 262365, 1 specimen, Gabon, Ogowe-Ivindo, WCTS Forestry Concession, Site 2.

DISCUSSION

In a recent survey of the Mfimi River, collections were made principally at sites along the main channel, but some peripheral habitats were also sampled and among these were a small collection made in the Ndzaa River. Although a full accounting of fish diversity and distribution throughout the region remains to be made, preliminary data indicate that small left bank tributaries of the Mfimi-Lukenie appear to harbor a high proportion of the region's fish diversity (Stiassny et al., personal obs.). Although just two collections were made in the Ndzaa, and despite its relatively small size, 27 species are recorded, of which nine were not collected elsewhere within the

basin (indicated in bold font, table 1), and among these were the two new species of *Phenacogrammus* described here. These first ichthyological collections in the Ndzaa hint at the potential for additional undescribed diversity in these affluent small stream habitats. Anthropogenic impacts in Lake Mai-Ndombe and along the Mfimi-Lukenie main channel include poorly regulated fisheries, extensive clearance of seasonally inundated forests for rice cultivation and logging, and all are increasingly impacting the aquatic system (Thieme et al., 2005; Stiassny et al., 2011). Currently such anthropogenic impacts appear to be minimal in many of the smaller southern tributaries, presenting an opportunity to fully document the ichthyofaunal diversity of the region while providing baseline data for focused conservation efforts.

The genus *Phenacogrammus* is one of the more poorly studied of alestid clades, and studies that have investigated phylogenetic relationships within the Alestidae, or more inclusively within the Characoidei, have been based exclusively on molecular data and incorporated few, if any, *Phenacogrammus* species (e.g., Calcagnotto et al, 2005; Arroyave and Stiassny, 2011; Melo et al., 2021), leaving generic intrarelationships unresolved. Our preliminary investigation of morphological variation within the genus recognizes a peculiar expansion of first pleural rib present uniquely in *P. flexus*, *P. concolor*, and *P. deheyeni*, a feature interpreted here as a synapomorphy diagnostic of this small central Congolese subgroup. In terms of overall phenetic similarity, *P. concolor* is closer to *P. deheyeni* than to *P. flexus*, but additional morphological and molecular data are needed to definitively resolve these relationships, and a comprehensive taxonomic revision is necessary to properly delineate all species within the genus.

As noted previously *P. flexus* and *P. concolor* are currently known only from their type locality in the Ndzaa River, however a preliminary SDM (species distribution modelling) analysis conducted in Wallace, a modular, R-based platform for modeling of species niches and distributions (Kass et al. 2018), predicts the presence of highly suitable habitat for both species in the nearby headwaters of the Ulanzaa River basin (fig. 1). Future surveys planned in both the Ndzaa and Ulanzaa catchments will help test this prediction and provide additional data for modelling these and other species distributions throughout this poorly documented, yet potentially species-rich region.

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TABLE 5. Morphometric measurements and meristic data for the holotype and four paratypes of *Phenacogrammus concolor*, new species. Mean values include measurements of the holotype.

Morphometric measurements	Holotype	Paratypes		
		mean	max	min
Standard length (mm)	43.9		42.9	34.5
% SL				
Body depth	25.4	24.9	27.3	23.6
Head length	21.5	21.7	25	20.2
Dorsal-fin base	10.9	11.5	13.7	9.5
Anal-fin base	16.8	18.3	22.3	16.8
Predorsal length	51.7	52.6	54.5	51.3
Preanal length	68.9	69.2	69.9	68.4
Prepelvic length	47.4	48.2	50.4	44.1
Caudal peduncle length	37.9	36.3	37.9	34.5
Caudal peduncle depth	10.4	10.4	10.9	9.6
% HL				
Eye diameter (bony orbit)	43.2	44.8	46.9	41.4
Upper jaw length	43.2	42.7	45.8	39.1
Lower jaw length	49.5	50.1	55.2	43.8
Snout length	29.5	28.3	29.9	25.3

Meristic counts	Holotype	mode	max	min
Total vertebral count	32	31	33	31
Dorsal-fin rays	ii7	ii7	ii8	ii7
Anal-fin rays	iii15	iii15	iii16	iii15
Pored lateral line scales	6	6	7	5
Longitudinal scales	27	28	28	26
Scales to dorsal-fin origin	3	4	4	3
Scales to pelvic-fin insertion	3	3	3	3
Circumpeduncular scale rows	10	10	10	10

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