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Hidden species diversity in the *Enteromius* Cope, 1867 (Teleostei: Cyprinidae) from the Aruwimi basin (Middle Congo) in the Okapi Wildlife Reserve (Democratic Republic of the Congo)

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Abstract

Two new African minnow species, *Enteromius cerinus* sp. nov. and *Enteromius ruforum* sp. nov., are described for science from the Angadiko River, a left-bank sub-affluent of first order of the Nepoko River, draining the north-eastern part of the Okapi Wildlife Reserve (OWR). Both new species belong to the group of *Enteromius* for which the last unbranched dorsal-fin ray is flexible and underrated. Within this morphological group, both are most similar to *Enteromius kamolondoensis*, especially in life colour pattern characteristics. However, *Enteromius cerinus* sp. nov. differs from *E. kamolondoensis* by its low number of circumpeduncular scales, 10–11 (vs. 12), low maximum body depth, 22.8%–25.7% standard length (L_s) (vs. 26.1%–30.0%), and long anterior and posterior barbel lengths, 32.6%–35.3% head length (L_H) (vs. 23.6%–27.2%) and 41.6%–43.9% L_H (vs. 30.3%–34.9%), respectively. Further, *E. ruforum* sp. nov. is also easily distinguished from *E. kamolondoensis* by its high maximum body depth, 30.6%–33.3% L_s (vs. 26.1%–30.0%), and small, isometric, eye diameter, 26.2%–28.0% L_H (vs. 29.1%–31.9%). A barcoding study (mtDNA, cytochrome oxidase subunit I [*COI*]) revealed that specimens of both new species form lineages well differentiated from those of other available species. As such, (i) *E. cerinus* sp. nov. diverges from *E. kamolondoensis* by a K2P genetic distance (GD) of 10.3% and (ii) *E. ruforum* sp. nov. by a K2P GD of 11.2%. To the present day, the fish fauna of the left-bank sub-affluents of the Nepoko River, in general, remains poorly known or

undocumented. Unfortunately, at the same time, multiple anthropogenic impacts are affecting this fauna, such as (i) the destruction of habitats along the river banks for agriculture and fishing and (ii) the use of illegal fishing practices, such as fishing with plant-based ichthyotoxins during ecopage, which is combined with dam building. As a result of the demographic growth, this ecopage results in overfishing and thus is threatening both new species in particular, but all other co-occurring fish species as well. Both new species, *E. cerinus* sp. nov. and *E. ruforum* sp. nov., should thus be considered Vulnerable (VU) according to IUCN criterion D2. It is therefore hoped that their discovery highlights the urgent need for a better protection and further in situ exploration of the reserve's freshwater (fish) biodiversity, in general, and that of those small sub-affluents, in particular.

KEYWORDS

COI barcoding, conservation, *Enteromius cerinus* sp. nov., *Enteromius ruforum* sp. nov., Middle Congo, Nepoko River

1 | INTRODUCTION

With an estimated total of 1785 valid species, distributed over 160 valid genera (Fricke et al., 2024), the family Cyprinidae is one of the largest freshwater fish families in the world. Species of this family are widely represented in North America, Africa, Europe, and Asia but are naturally absent from South America, Madagascar, and Australia. Nevertheless, some species have been the subject of multiple voluntary introductions by humans, extending beyond the borders of their natural distribution (Berra, 2007; Bruslé & Quinard, 2001). Many species are difficult to identify, which is especially true for those of the cyprinid genera *Enteromius*, *Labeo*, and *Labeobarbus*. This results from their high alpha-taxonomic diversity, high morphological similarity, and the lack of recent identification keys (Kisekelwa et al., 2022; Lévêque, 1989a; Liyandja et al., 2022; Van Ginneken et al., 2017; Vreven et al., 2018).

The genus *Enteromius* Cope 1867, formerly referred to as African small '*Barbus*', occurs only in the African continent and contains, to date, 229 valid species (Froese & Pauly, 2024), of which 122 species are known from the Congo basin sensu lato (*s.l.*), that is, including the Lake Tanganyika basin with all its affluent rivers and Lake Kivu as well (De Vos & Snoeks, 1994; Snoeks, 2000). Although paraphyletic and probably composed of several lineages (Agnèse et al., 1990; Hayes & Armbruster, 2017; Oellermann & Skelton, 1990; Yang et al., 2015), with this high number of species, the genus *Enteromius* is, to date, among the most species-rich of the riverine African freshwater fish genera. Nevertheless, it still seems to contain hidden species diversity, especially in poorly or unexplored basins and areas. Indeed, several recent studies revealed undescribed *Enteromius* species; these often hidden in large species complexes in need of further study (Hayes & Armbruster, 2017; Katemo Manda et al., 2020; Kisekelwa et al., 2022; Maetens et al., 2020; Schmidt et al., 2017; Van Ginneken et al., 2017; Yang et al., 2015).

The Okapi Wildlife Reserve (OWR), a protected area created on May 2, 1992, and situated in the north-east of the Democratic Republic of the Congo (DRC) (Figure 1), covers a forest area of about 13,726 km^2 (IUCN/WCMC, 1995). In 1996, the reserve was placed on the World Heritage List of the UNESCO on the basis of its exceptional biological value. In 1997, it was inscribed on the list of World Heritage as in Danger and has remained listed on it since. This was, originally, due to civil wars (1996–2002), resulting in major illegal activities, such as poaching, mining, and an increased migration of people from out- to inside the reserve, with a significant negative impact on the reserve (UNESCO, 2010). To date, these ongoing illegal activities result in that the OWR remains in the list of World Heritage as in Danger.

At the time of its inscription as site on the World Heritage List, that is, 1996, our knowledge of the fauna of the OWR mostly concerned large mammals and birds. Indeed, its main protection focus included the okapi [*Okapia johnstoni* (Sclater 1901)] and its habitat, but also the chimpanzee [(*Pan troglodytes* (Blumenbach 1776)], aquatic genet [*Genetta piscivora* (Allen 1919)], giant genet [*Genetta victoriae* (Thomas 1901)], congo peafowl (*Afropavo congensis* Chapin 1936), and grey parrot (*Psittacus erithacus* Linnaeus 1758). In addition, the reserve is home to 17 species of primates, including the aforementioned chimpanzee, which is the largest number of species for a single forest block in Africa (UNESCO, 2010). Nevertheless, other groups, such as fish, remained scientifically poorly documented, with only 58 species known (RMCA Collection, 2009), but unpublished upon. Our knowledge of the latter has greatly improved after a more in-depth study of existing collections and amounts, currently, to 121 species (Decru et al., 2017). This ichthyofauna also includes a few endemic species such as *Labeobarbus macroceps* (Fowler, 1936) and *Brycinus epuluensis* Decru et al. (2016), both endemic to the Epulu River.

The reserve is legally inhabited by humans of both Bantu and Pygmy ethnic origins. In 1995, the Institut Congolais pour la Conservation de la Nature (ICCN), World Wildlife Fund (WWF), Wildlife Conservation Society (WCS), and Wildlife Conservation Global (WCG) recommended several strategies to face the various anthropogenic

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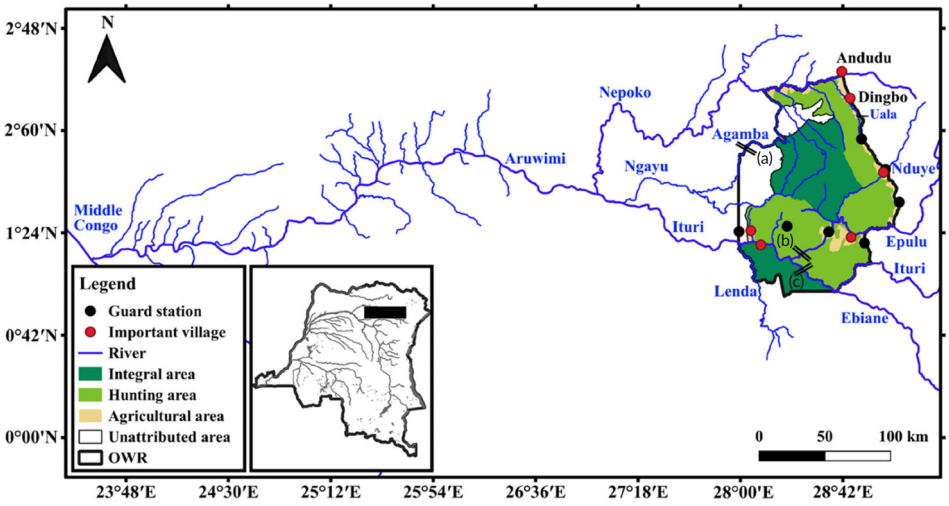


FIGURE 1 Situation of the Okapi Wildlife Reserve (OWR) within the Congo basin and the Democratic Republic of the Congo (DRC) with details on its hydrography and protection versus human use areas. Double black bars indicate main waterfalls with (a) Agamba Falls (on the Agamba River), (b) Arabia Falls (on the Epulu River), and (c) Ituri Falls (on the Ituri River).

threats in the reserve (RFO, 2004). One of the main strategies adopted was to divide the reserve into protection versus human use areas to guarantee to the local human populations their user rights, while also respecting the status of the OWR as a protected area (PA). As such, the reserve was divided into four types/categories of areas (Figure 1): (i) integral areas (IAs), covering two distinct zones, one in the center and another in the south of the reserve, where all human activity is strictly prohibited; (ii) hunting areas (HAs), where only some traditional methods are allowed to cover the subsistence needs of the indigenous populations in terms of hunting (mammals) and fishing (fishes) products; (iii) agricultural areas (AAs), where humans are allowed to cultivate crops such as the cassava plant (manioc) (Euphorbiaceae), and which are mainly located toward the borders of the reserve and along the main roads; and finally (iv) unattributed areas (UAs), being areas not yet attributed to one of the above and located in the western-most part of the reserve (IUCN/WCMC, 1995).

Some of the rivers draining the OWR were first explored by Hebert Lang and James Chapin (1907–1913) of the American Museum of Natural History (AMNH), and subsequently by George Vanderbilt in 1934 (Fowler, 1936). Several years later, the Belgian ichthyologist Luc De Vos (1990) explored the Epulu River, followed by a series of expeditions (2009 onward) organised mainly by researchers from the University of Kisangani (UNIKIS: DRC) and the RMCA (Belgium), then in 2010, by other researchers from UNIKIS and the Cornell University Museum of Vertebrates (Ithaca, NY, USA).

A total of nine species of *Enteromius* have been listed based on those explorations (Decru et al., 2017; Van Ginneken et al., 2017). Of those, four have the last unbranched dorsal-fin ray bony and serrated: *Enteromius* cf. *apleurogramma* (Boulenger, 1911), *Enteromius miolepis* (Boulenger 1902), *Enteromius* cf. *pellegrini* (Poll 1939), and *Enteromius trinotatus* (Fowler, 1936). Instead, the five remaining species have the last unbranched dorsal-fin ray flexible, simple and not serrated: *Enteromius atromaculatus* (Nichols & Griscom, 1917), *Enteromius* cf. *brazzai* (Pellegrin 1901), *Enteromius humeralis* (Boulenger 1902), *Enteromius jae* (Boulenger, 1903), and *Enteromius* sp. '10 cps'. It is to be noted that the last species remains to be described for science, whereas three of them are indeed similar to already known species but seem, nevertheless, somewhat different and thus in need of further alpha-taxonomic attention.

During recent field expeditions targeting the rivers draining the eastern border of the OWR (2019–2020), several series of *Enteromius* specimens were collected in the Uala basin, situated in the north-eastern part of the reserve and a left-bank affluent of the Nepoko River, the latter river forming the northern border of the reserve and itself being a right-bank affluent of the Aruwimi/Ituri (Figure 1).

Based on (i) the structure of last unbranched dorsal-fin ray, that is, flexible, simple, and thus not serrated, and (ii) the body colouration, characterised by the presence of a permanent midlateral black band on the flanks, three series of specimens have been identified during these recent expeditions. Among these species, two are here preliminary named *Enteromius* sp. 'angadiko 1' and *Enteromius* sp. 'angadiko 2', both originating from the Angadiko River, that is, a left-bank sub-affluent of the fourth-order Nepoko River, whereas the third one is named *Enteromius* sp. 'uala', after the Uala River, a left-bank affluent of the Nepoko River itself. All three of them revealed to be most similar to *Enteromius kamolondoensis* (Poll, 1938), a species originally described from the Upper Congo basin (Upper Lualaba), in the Kamalondo Depression (USBGN, 1964) (or Kamolondo Depression; Upemba National Park), between the Lake Kasibasiba channels at Bukama Town, the Luvua River at Kiambi Town, and the Lukusi River at Manono Town (Poll, 1938). The distribution area for this species, indeed, covers the Upper Lualaba section of the Congo basin, although additional specimens have been identified further downstream from the Malembia River, a right-bank sub-affluent of the Upper Congo/Lualaba near Kibombo Village (3°53′40.7″ S–26°03′18.3″ E at 482 m altitude) (Froese & Pauly, 2024; Lévêque & Daget, 1984; Poll, 1976).

However, it is to be noted that the greyish-black midlateral band of the specimens from the Uala River, here named *Enteromius* sp. 'uala', revealed not to be permanent (see discussion). As such, these specimens need comparison with both kind of species, that is, those with and without a black midlateral band, which is not needed for the other two series of specimens, that is, those named *Enteromius*

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sp. 'angadiko 1' and *Enteromius* sp. 'angadiko 2'. Therefore, the specimens of the Uala River are further dealt with in a separate paper (Mayo Ilodiri et al., submitted).

A thorough morphological study of both series of specimens from the Angadiko River revealed that they differ from *E. kamolondoensis* by (i) colouration, (ii) some meristics, and (iii) some morphometrics. These results were complemented and confirmed by a *COI* barcoding genetic approach (mtDNA). Accordingly, both series of specimens (*Enteromius* sp. 'angadiko 1' and *Enteromius* sp. 'angadiko 2') are here formally described as two new species for science and named, respectively, *Enteromius cerinus* sp. nov. and *Enteromius ruforum* sp. nov. Moreover, various severe anthropogenic impacts to the rivers, such as the destruction of habitats along the river banks for agriculture, fishing, and the use of illegal fishing practices, such as fishing with plant-based ichthyotoxins during ecopage fishery, which is combined with dam building, have been documented and discussed. Finally, the importance of these discoveries highlights the urgent need for (i) a better knowledge of the ichthyofauna of all the rivers draining the reserve as a whole and (ii) a better protection of this freshwater ichthyofauna of the OWR.

2 | MATERIALS AND METHODS

2.1 | Ethics statement

Sampling was authorised by the managers of the OWR, that is, the ICCN and the traditional chiefs. The authorizations of the ICCN have also allowed us to use gillnets of small mesh-size (8, 10, 12, and 15 mm) and landing nets in accordance with the derogation provided for scientific purposes in articles 19 and 20 of the law of the DRC N°14/003 of February 11, 2014, on nature conservation. Live specimens were further anaesthetised using clove oil in accordance with the European Directive 2010/63/EU on the protection of animals used for scientific purposes (see Annex IV in Directive 2010/63/EU).

2.2 | New collections

Specimens of both the new species were collected during recent field expeditions (2019, 2020, and 2022) in the north-eastern part of the OWR. During sampling, fish were caught using various fishing methods, including gillnets of small mesh-size (8, 10, 12, and 15 mm), fyke, and landing nets. Some selected specimens were photographed in a field aquarium. From anaesthetised specimens, a fin clip of the right pelvic fin and, whenever needed, of the right pectoral fin was taken per specimen and preserved in 96% ethanol for further molecular analysis. Specimens themselves were fixed in 10% formalin before being transferred to 70% ethanol for long-term preservation at the RMCA. To link a specimen and its fin clip(s), a permanent tag was attached to fin-clipped specimens, bearing a unique number.

All locality data have been translated into English. Following the current policy for renaming original RMCA collection numbers, former RMCA collection numbers A0 up to A9 are now listed as RMCA 2000–2009 and former numbers B0 up to B6 as RMCA 2010–2016.

2.3 | Morphological data

A total of 48 *Enteromius* specimens were examined, including 16 specimens of *Enteromius* sp. 'angadiko 1' and 13 specimens of *Enteromius* sp. 'angadiko 2', both from the Angadiko River in the north-eastern part of the OWR, Middle Congo, 6 out of the 23 syntypes, and 13 non-type specimens of *E. kamolondoensis*, all from the Upper Congo/Lualaba River (see list of comparative material).

Thirteen counts and 23 point-to-point measurements (Figure S1) were taken on the left-hand side of each specimen, except in cases where damage necessitated the use of the right-hand side, most following Bamba et al. (2011), and two additional measurements following Katemo Manda et al. (2020), that is, the anterior and posterior barbel lengths. As such, both vertebral counts were taken from radiographs using the VisiX equipment (Medex Loncin S.A., 2011), performed at the RMCA, following Katemo Manda et al. (2020). All measurements on the head were expressed in percentage of head length (L_H), whereas measurements on the body were expressed in percentage of standard length (L_s). Counts and measurements were taken under a Nikon binocular with electronic caliper to the nearest 0.1 mm.

Data were examined using multivariate principal component analyses (PCA). Counts and measurements were analysed separately. For counts, the raw data were used and the analysis was performed on the correlation matrix. For the measurements, the log-transformed data were used and the analyses were performed on the covariance matrix (Bookstein et al., 1985; Somers, 1986). As the first axis of the latter PCAs can, indeed, be interpreted as mainly a proxy for size (Bookstein et al., 1985), the second and third axes were further evaluated. Five counts were not included in the PCA because they were invariable, that is, the number of (i) lateral-line dorsal-fin origin scales, (ii) lateral-line pelvic-fin origin scales, (iii) dorsal-fin rays, (iv) anal-fin rays, and (v) principal caudal-fin rays.

Non-parametric Mann–Whitney *U*-tests (MW*U*-tests), with sequential Bonferroni correction (Armstrong, 2014; Rice, 1989), were used for univariate comparisons between the studied groups/species. Nevertheless, these tests were not performed between groups/species for which fewer than five specimens were available per group/species and/or for which their *L*s were significantly different ($p \leq 0.5$) between groups/species. The diagnostic value of the (highly) significantly different variables was explored using simple scatterplots of the individual variable (in $\%L_H$ or $\%L_S$) against size (in millimeters), that is, L_H for measurements taken on the head and L_S for measurements taken on the body, to visualise the degree of overlap. Statistical analyses were performed with PAST version 3.26 (Hammer et al., 2001) and STATISTICA version 8.0 for Windows from StatSoft. Inc. (www.statistica.com).

The last unbranched dorsal-fin ray revealed to be flexible, simple, and not serrated in the specimens of both the new species. In

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addition, their colouration and colour pattern are characterised by being overall brownish or yellowish and pale toward the belly and the ventral surface of the head, and the presence of a black midlateral band on the flanks. As such, both the new species are most similar to *E. kamolondoensis* with which they have been compared in full detail. Therefore, PCA on the meristic and morphometric data and also MW *U*-tests on both datasets were first performed with that species included. However, considering the fully non-overlapping results of the PCA on the meristics and the lack of any added value of the MW*U*-tests beyond the obvious non-overlapping differences between species, further details for that PCA and those MW*U*-tests are not presented (see also Kashindye et al., 2021; Katemo Manda et al., 2021, 2023).

In the comparative diagnosis, both the new species were first compared to their 65 congeners from the Congo basin *s.l.* using the updated list of species whose last unbranched dorsal-fin ray is flexible and not serrated, as provided by Katemo Manda et al. (2020). Further comparison with the *Enteromius* species from the south-western part of the Upper Nile ecoregion (Abell et al., 2008; Thieme et al., 2005), that is, the Nile basin, was also provided as this part of the Nile basin borders the Aruwimi/Ituri headwaters to the east of the OWR. It was delimited as the drainage region thattakes lakes Edward and George, the Semliki River, Lake Albert, and the Albert Nile as far downstream as Mongalla Town where a large swamp (Sudd) area starts. In addition, it includes the major right-bank affluent of the Albert Nile, which connects to Lake Victoria, but below the Murchison Falls. This is the area situated approximately between 0 and 5° north latitude and 28 and 32° east longitude (Dumont, 2009: Figure 1; ICAR World Bank Report, 2013: annex 9). This comparative list of *Enteromius* species of the Upper Nile, containing a total of six valid species, was compiled based on information available in several key publications [see Decru et al., 2019; Froese & Pauly, 2024; Lévêque, 1989b; Maetens et al., 2020; and Neumann et al., 2016 (Table S1)].

The values for counts and measurements obtained in the present study were used in the comparative diagnosis for both the new species (see list of comparative material). Other data provided in both diagnoses are extracted from the original descriptions of the species with which the two were compared, that is, Boulenger (1903, 1911, 1916), David and Poll (1937), De Vos (1991), Katemo Manda et al. (2020), Lambert (1961), Maetens et al. (2020), Matthes (1964), Nichols and Griscom (1917), and Poll (1938).

2.4 | Molecular data, DNA analyses

The mitochondrial cytochrome oxidase subunit 1 gene (*COI*) of 16 individuals [four *Enteromius* sp. 'angadiko 1', three *Enteromius* sp. 'angadiko 2', four *E. kamolondoensis*, and five *Enteromius* sp. 'uala', the latter, a third undescribed species from the OWR whose original description is in preparation (W.M.I., personal data)] was sequenced.

DNA was extracted from fin clips using the Nucleospin® Tissue Kit (Macherey-Nagel™, Germany), following the manufacturer's protocol. The *COI* gene was amplified with PCR, using the universal M13-tailed primer, used for fish DNA barcoding (Ivanova et al., 2007). The PCR had a total reaction volume of 23.5 μL for each sample on the plate. The reaction mix contained 2.5 μL PCR buffer (10x), 2.5 μL dNTP (2 mM), 1.25 μL primer cocktail (2 μM), 0.2 μL Taq DNA polymerase (5 units per microliter), 17.75 μL mQ-H_2O, and 1 μL extracted DNA. The PCR profile started with an initial denaturation at 94°C for 180 s, followed by 35 cycles of denaturation at 94°C for 45 s, annealing at 51°C for 40 s and extension at 72°C for 90 s, and concluded with a final extension at 72°C for 600 s (Decru et al., 2016). The PCR product was checked using a 1.5% agarose gel with Midori Green direct (FastGene®). The product was further purified using the ExoSAP-IT™ PCR Cleanup kit (Affymetrix, Inc., USA) following the manufacture's protocol. The Standard Sanger sequencing was done bidirectionally using the ABI 3730XL capillary sequencer. The sequences were quality checked, assembled, and cleaned in Geneious Prime® 2020.1.2 (Biomatters Ltd.).

Sequences were aligned in MEGA 11.0.10 (Tamura et al., 2021). All newly generated sequences ($n = 16$) were combined and aligned with 418 partial *COI* sequences of *Enteromius* downloaded from GenBank, and 35 additional *Enteromius* sequences from other studies that yet have to be released on GenBank (7 *Enteromius* sp. 'ascutelatus', 7 *Enteromius quadrilineatus*, 2 *Enteromius lineomaculatus* from the Ruzizi, 8 *E. lineomaculatus* from the Malagarasi, 5 *Enteromius* cf. *unitaeniatus* from the Upper Congo basin, and 6 *E.* cf. *unitaeniatus* from the Lower Congo basin), to generate an initial global maximum likelihood (ML) phylogenetic tree.

Among the *COI* sequences downloaded from GenBank, some specimens had to be reexamined and possibly (re)identified. This is the case of four specimens previously identified and labeled as follows: *E.* cf. ($n = 2$; KT193048.1, KT193080.1; RMCA 2010-09-DNA-634-uncat, RMCA 2010-09-DNA-7449-uncat), *Enteromius* sp. 'Congo' ($n = 1$; KT193060.1; RMCA 2010-09-DNA-17F7-uncat), and *Enteromius* sp. 'Loboya' ($n = 1$; KT193062.1; RMCA 2010-09-DNA-19C3-uncat). All these specimens were found to be conspecific in the original ML phylogenetic tree (Figure S2). All four specimens are most similar to *E. atromaculatus* in their colouration pattern with three small spots on the flanks. After re-identification of these specimens, they differed from *E. atromaculatus* on the basis of the following morphological characters: 10 scales around the caudal peduncle (vs. 12); 3.5 scales between the lateral and dorsal line (vs. 4.5), and 23–24 scales on the lateral line (vs. 26). Thus, they were all (re)identified as *E.* cf. *atromaculatus*.

Systomus sarana (Hamilton 1822), an Asian cyprinid species (tribe: Smiliogastrini), was selected as an outgroup to *Enteromius* ($n = 3$) (see Hayes & Armbruster, 2017; Ren & Mayden, 2016; Yang et al., 2015). All sequences were trimmed to a corresponding final length of 558 bp. The ML tree was constructed using the best-fit model selected based on the AIC criterion (Akaike, 1974; Kumar et al., 2016) and 300 bootstrap replications. To further concentrate the focus on the branches of interest for this study in the ML tree, an ML subtree was compiled using (i) the newly generated sequences, (ii) the sequences of those species that revealed to be sister group(s) to these newly generated sequences and this with a bootstrap value of at least 75% in the original tree, and (iii) the outgroup.

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Further, average Kimura 2-parameter (K2P) (Kimura, 1980) and uncorrected p (Srivathsan & Meier, 2012) genetic distances (GDs) between the sequences for the different species retained in the subtree were computed in MEGA. These two-distance metrics are routinely reported in DNA barcoding studies and, thus, enable direct comparison with other studies (see also Bektas et al., 2018; Levin et al., 2018). Both values are reported, because K2P-distances tend to exaggerate species delimitation based on closely related sequences, whereas the uncorrected p-distances do not account for multiple mutation hits in strongly divergent sequences (Srivathsan & Meier, 2012).

Tissue vouchers are deposited at the RMCA, and newly obtained sequences were deposited in GenBank for future reference (Table S2). The holo- and para-genetypes were also designated following the definitions of Chakrabarty (2010).

2.5 | Nomenclatural acts

According to the International Code of Zoological Nomenclature (ICZN) as currently amended, the name of the two new species described herein is available under this code from the electronic edition of this article. This published work and the nomenclatural acts it contains have therefore been registered in the ICZN online registration system, ZooBank. The ZooBank Life Science Identifier (LSID) is available, and the associated information can be accessed through any standard web browser by appending the LSID to the prefix 'http://zoobank.org/'. The LSID of the present publication is urn:lsid:zoobank.org:pub: 86B73E04–1741-4A28-BE66-035ADC3A7035.



FIGURE 2 Photographs of the lateral view of a live specimen of (a) *Enteromius kamolondoensis*, RMCA 2016-25-P-uncat, 45.4 mm L_S, Upper Congo, Kalule Nord River (August 26, 2016); (b) *Enteromius* sp. "angadiko 1" (= *Enteromius cerinus* sp. nov.), holotype, RMCA 2019-019-P-0041, 43 mm L_S, Middle Congo, Angadiko River, a sub-affluent of the left bank of the Nepoko River, near Dingbo Village (July 29, 2019); and (c) *Enteromius* sp. "angadiko 2" (= *Enteromius ruforum* sp. nov.), paratype, RMCA 2019-019-P-0074, 48.7 mm L_S, Middle Congo, Angadiko River, a sub-affluent of the left bank of the Nepoko River, near Dingbo Village (July 29, 2019).

3 | RESULTS

3.1 | A brief overview on the colouration and colour pattern differences

During the present study, both potentially new species from the OWR, *Enteromius* sp. 'angadiko 1' and *Enteromius* sp. 'angadiko 2', revealed to be most similar to *E. kamolondoensis* based on the following characteristics: (i) the morphology of last unbranched dorsal-fin ray flexible and unserrated and (ii) their overall colour pattern, with the presence of a black midlateral band (Figure 2). However, four qualitative colour pattern characters, including the midlateral band itself as one of them, have been documented to differentiate these three (potential) species (Table 1).

3.2 | Documenting meristic differences

As several meristics revealed to be obviously diagnostic, considering there is even no overlap between values and/or ranges, no PCA and MWU-test results are presented here (see Section 2 for more details). Among the meristics, indeed, there are several non-overlapping ones that revealed to be good discriminating, that is, diagnostic, characters between both the (potential) new species and *E. kamolondoensis*. As such, the first (potential) new species, *Enteromius* sp. 'angadiko 1', can readily be distinguished from *E. kamolondoensis* by two meristics: (i) a lower number of pectoral-fin rays, 12–13 (vs. 15–16) and (ii) a lower number of circumpeduncular scales, 10–11 (vs. 12). Furthermore, the second (potential) new species, *Enteromius* sp. 'angadiko 2', can also readily be distinguished from *E. kamolondoensis* by three meristics: (i) a lower number of lateral-line scales, 24–26 (vs. 27–30); (ii) a lower total number of vertebrae, 26–27 (vs. 28); and (iii) a lower number of abdominal vertebrae, 13 (vs. 14). Finally, the two potentially new species, *Enteromius* sp. 'angadiko 1' and *Enteromius* sp. 'angadiko 2', can be distinguished from each other based on two meristics: the number of circumpeduncular scales, 10–11 (vs. 12, respectively) and the number of pectoral-fin rays, 12–13 (vs. 14–15).

3.3 | Documenting morphometric differences

A first PCA was performed on 23 log-transformed measurements for all examined specimens ($n = 48$). The highest loadings on PC II are for anterior and posterior barbel lengths, maximum body depth, minimum caudal peduncle depth, eye diameter, and minimum body depth. The highest loadings on PC III are for eye diameter, anterior barbel

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TABLE 1 Description of the character state for the four qualitative colour pattern related characters as studied in *Enteromius kamolondoensis*, *Enteromius* sp. 'angadiko 1', and *Enteromius* sp. 'angadiko 2" (see Figure 2a–c).

	Qualitative characters			
Species	**Midlateral band: length, colour, and height**	**Operculum**	**Lateral line scales**	**Base of caudal peduncle**
Enteromius kamolondoensis	Incomplete, runs from the upper, posterior, end of the operculum to the caudal-fin base; greyish; less broad, about half a scale in height	No spot	With a series of black, chevron-shaped markings	With a weak blackish spot
Enteromius sp. 'angadiko 1"	Complete, runs from tip of snout to the caudal-fin base; greyish-black and well-marked; broad, about one scale in height and sometimes encompassing three black spots on the flanks	With a large black spot	With a series of black, chevron-shaped markings	With a weak black spot
Enteromius sp. 'angadiko 2"	Incomplete, runs from the upper, posterior, end of the operculum to the caudal-fin base with a distinct black spot; blackish and well-marked; less broad, about half a scale in height	With a large black spot	No series of chevron-shaped markings	With a well-distinct black spot

TABLE 2 (a) Variable loadings for the second and third principal axes of a principal component analysis (PCA) carried out on 23 log-transformed measurements for all examined specimens ($n = 48$). The most important variables are in bold. (b) Results of the Mann–Whitney *U*-tests (MW*U*-tests) between *Enteromius* sp. 'angadiko 1' (ang1) (= *Enteromius cerinus* sp. nov.), *Enteromius kamolondoensis* (kam), and *Enteromius* sp. 'angadiko 2' (ang2) (= *Enteromius ruforum* sp. nov.) for the 23 measurements included in PCA.

	a. PC loadings		b. MW*U*-tests	
Measurements	**PC II (13.9%)**	**PC III (6.1%)**	**ang1 vs. kam (*n*: 13 vs. 11)**	**ang2 vs. kam (*n*: 8 vs. 11)**
Standard length	0.04052	0.08736	0.83927	0.74118
Head length	−0.01523	**0.31952**	*0.00029*	0.05754
Pre-dorsal distance	−0.03477	−0.04596	0.36907	*0.00052*
Dorsal-caudal distance	0.13537	0.07314	**0.00129**	0.80435
Post-dorsal distance	0.06505	−0.19541	*0.00009*	*0.00028*
Dorsal-fin base length	0.17286	−0.06195	*0.00007*	0.36372
Dorsal-fin length	0.09459	−0.02829	**0.03442**	0.09865
Prepectoral distance	−0.05262	**0.23592**	*0.00046*	0.08292
Pre-pelvic distance	−0.04062	0.05439	**0.00106**	**0.03899**
Pre-anal distance	−0.00579	0.01383	0.06794	**0.01324**
Anal-caudal distance	0.17775	0.22757	**0.01618**	**0.00385**
Post-anal distance	0.18953	−**0.27756**	*0.00012*	0.24768
Minimum body depth	−**0.23355**	−0.07011	*0.00003*	*0.00028*
Maximum body depth	−**0.27114**	−**0.26127**	*0.00019*	*0.00028*
Maximum caudal peduncle depth	−0.18894	−0.21896	**0.01893**	*0.00052*
Minimum caudal peduncle depth	−**0.26459**	−0.13319	*0.00003*	*0.00028*
Preoccipital distance	0.15409	0.20782	*0.00003*	*0.00028*
Eye diameter	**0.24641**	**0.48247**	*0.00003*	*0.00028*
Snout length	0.15189	−0.05786	*0.00003*	*0.00028*
Preoperculum distance	0.01909	0.17032	*0.00003*	0.36372
Interorbital width	−0.06909	**0.25271**	0.17326	*0.00028*
Anterior barbel length	**0.51228**	−**0.34945**	*0.00003*	*0.00028*
Posterior barbel length	**0.50467**	−0.13859	*0.00003*	*0.00028*

Note: Significant, $p \leq 0.05$ (bold), and highly significant, $p \leq 0.001$ (italics), values after sequential Bonferroni correction. For the size class between species : (i) ang1 vs. kam ($L_S = 39.1–47.2$ vs. 39.0–48.6) and (ii) ang2 vs. kam ($L_S = 43.7–52.8$ vs. 42.9–52.5).

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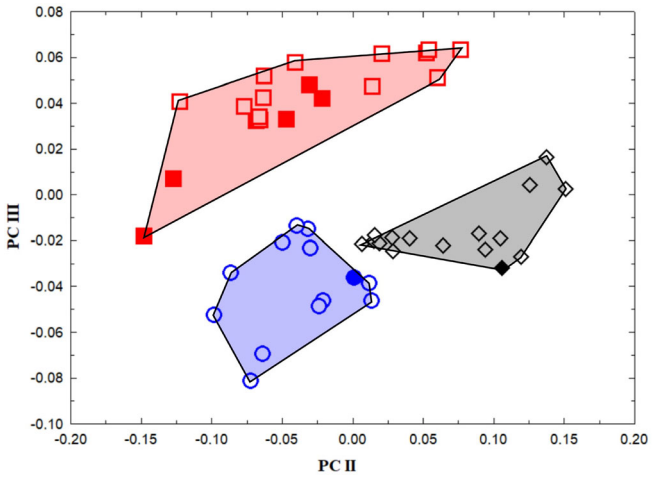


FIGURE 3 Scatterplot of PC II against PC III for a principal component analysis on 23 log-transformed measurements of all examined specimens ($n = 48$). *Enteromius* sp. "angadiko 1" (=*Enteromius cerinus* sp. nov.): ◆, holotype, ◇ paratypes; *Enteromius kamolondoensis* ■, syntypes, □, other specimens; and *Enteromius* sp. "'angadiko 2"' (=*Enteromius E. ruforum* sp. nov.): ●, holotype, ○, paratypes.

length, head length, post-anal distance, maximum body depth, interorbital width, and prepectoral distance (Table 2a).

A scatterplot of PC II against PC III revealed three well-distinct groups (Figure 3). A first group is mostly situated around the zero point of PC II, although with a bit more specimens toward its negative side, and largely on the positive side of PC III and contains the syntypes and specimens of *E. kamolondoensis*. A second group is situated entirely on the positive side of PC II and mostly on the negative side of PC III and contains the specimens of a first (potentially) new species, *Enteromius* sp. 'angadiko 1'. The third group is situated largely on the negative side of PC II and entirely on the negative side of PC III and contains the specimens of a second (potentially) new species, *Enteromius* sp. 'angadiko 2'.

MW *U*-tests with sequential Bonferroni correction were performed on all 23 measurements (Table 2b). These tests revealed that for the comparisons of (i) *Enteromius* sp. 'angadiko 1' against *E. kamolondoensis*, 19 measurements were found to be significantly different, 14 of which highly significant; and (ii) *Enteromius* sp. 'angadiko 2' against *E. kamolondoensis*, 15 measurements were found to be significantly different, 12 of which highly significant. Unfortunately, MW *U*-tests were not possible between the two (potentially) new species due to the lack of enough specimens (<5) of comparable size (L_S) for both. Indeed, most available *Enteromius* sp. 'angadiko 1' specimens are of smaller size (37.8–47.2 mm L_S) than those of *Enteromius* sp. 'angadiko 2' (43.7–60.0 mm L_S) (Figure 4a–d).

Based on scatterplots of the studied measurements, specimens of both (potentially) new species, *Enteromius* sp. 'angadiko 1' and *Enteromius* sp. 'angadiko 2', can be clearly distinguished from those of *E. kamolondoensis* by the following measurements: (i) *Enteromius* sp. 'angadiko 1' from *E. kamolondoensis* by a lower minimum body depth, 19.6%–22.4% L_s (vs. 22.6%–24.6%) (Figure 4a); a lower maximum body depth, 22.8%–25.7% L_s (vs. 26.1%–30.0%) (Figure 4b); a larger eye diameter, 32.4%–34.6% L_H (vs. 29.1%–31.9%) (Figure 4c); and a longer snout, 31.7%–34.6% L_H (vs. 27.9%–30.1%) (Figure 4d); and (ii) *Enteromius* sp. 'angadiko 2' from *E. kamolondoensis* by a higher minimum body depth, 24.7%–26.6% L_s (vs. 22.6%–24.6%) (Figure 4a); a higher maximum body depth, 30.6%–33.3% L_s (vs. 26.1%–30.0%) (Figure 4b); a smaller eye diameter, 26.2%–28.0% L_H (vs. 29.1%–31.9%) (Figure 4c); and a longer snout, 30.4%–33.2% L_H (vs. 27.9%–30.1%) (Figure 4d). It is interesting to note that both (potentially) new species differ from *E. kamolondoensis* for the same four measurements and in the same way, that is, deeper in *Enteromius* sp. 'angadiko 1' versus shallower in *Enteromius* sp. 'angadiko 2' for both body depths measured (see Figure 4a,b). Instead, they differ in the same way for the snout length, that is, it being longer in both (potentially) new species (Figure 4d), and in the opposite way for the eye diameter, that is, it being larger in *Enteromius* sp. 'angadiko 1' and smaller *Enteromius* sp. 'angadiko 2' (Figure 4c). Finally, specimens of both *Enteromius* sp. 'angadiko 1' and *Enteromius* sp. 'angadiko 2' can be distinguished from each other based on their minimum body depth, 19.6%–22.4% L_s (vs. 24.7%–26.6%) (Figure 4a); maximum body depth, 22.8%–25.7% L_s (vs. 30.6%–33.3%) (Figure 4b); and eye diameter, 32.4%–34.6% L_H (vs. 26.2%–28.0%) (Figure 4c). This seems to hold even if the specimens attributed to both the (potential) new species are mostly of a different size range (Figure 4a–c).

3.4 | Mitochondrial *COI* DNA-sequence analyses

The initial ML phylogenetic tree comprising all available *COI* barcoding sequences for *Enteromius* underscores that the specimens of both the potentially new species, *Enteromius* sp. 'angadiko 1' (= *E. cerinus* sp. nov.) and *Enteromius* sp. 'angadiko 2' (= *E. ruforum* sp. nov.), each formed distinct and well-supported clades [Bootstrap (BS) = 100], supporting the conspecificity of their specimens (Figure S2).

The generated subtree (Figure 5) contains a total of 39 specimens, with the sequences of both the (potentially) new species of this study and their well-supported sister group species (see Section 2 for more details). These include *E. atromaculatus* ($n = 9$), *Enteromius* sp. 'uala' ($n = 5$), *E. kamolondoensis* ($n = 4$), *E. lineomaculatus* with two distinct clusters, that is, one from the Malagarazi (Mal) ($n = 5$) and the other from the Ruzizi (Rus) ($n = 2$), a group of specimens here all (re)identified as *E.* cf. *atromaculatus* ($n = 4$) and with *S. sarana* ($n = 1$) as the outgroup.

The K2P GDs (Table 3) indicate that the *Enteromius* sp. 'angadiko 1' clade diverges from *E. kamolondoensis* by a K2P GDs of 10.3%. Instead, the *Enteromius* sp. 'angadiko 2' clade, being the sister group to the *E. atromaculatus* clade from the Epulu River basin (sequences accessed via GenBank), diverges from *E. atromaculatus* and from its morphologically most similar species, *E. kamolondoensis*, by a K2P GD of 3.8% and 11.2%, respectively.

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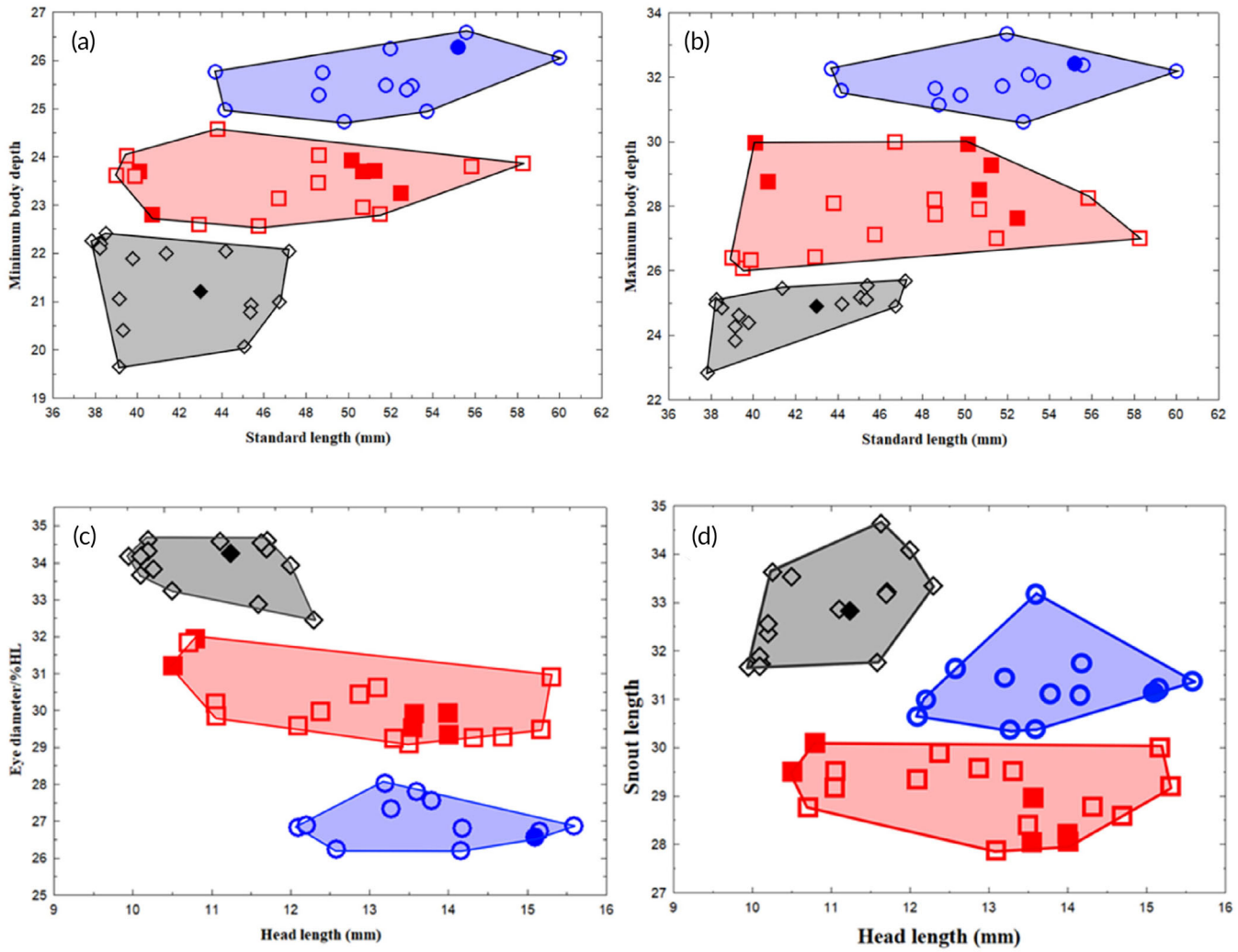


FIGURE 4 Scatterplots of (a) maximum body depth (%L_S) against standard length (in millimeters); (b) minimum body depth (%L_S) against standard length (in millimeters); (c) eye diameter (%L_H) against head length (in millimeters); and (d) snout length (%L_H) against head length (in millimeters). *Enteromius* sp. 'angadiko 1' (=*Enteromius cerinus* sp. nov.): ◆, holotype, ◇, paratypes; *Enteromius kamolondoensis*: ■, syntypes, □, other specimens; and *Enteromius* sp. 'angadiko 2' (=*Enteromius ruforum* sp. nov.): ●, holotype, ○, paratypes.

3.5 | Summary of the results of the integrative approach

The results obtained following an integrative approach using (i) colour pattern, (ii) meristic, (iii) morphometric, and (iv) genetic mtDNA barcoding data confirmed altogether, individually (i.e., for each approach separately) and also collectively, that the specimens belong to two distinct new species, for science, both originating from the Nepoko River subbasin (OWR). As such, they differ from each other and also from their most similar congeners and therefore represent, indeed, two new species for science. Both new species are described below and scientifically named *E. cerinus* sp. nov., for the specimens previously given the cheironym *Enteromius* sp. 'angadiko 1', and *E. ruforum* sp. nov., for those previously named by the cheironym *Enteromius* sp. 'angadiko 2'.

Additionally, common names are given in the local Mamvu and French and English languages. To highlight that because the common appellation 'petit barbeaux', 'petits *Barbus*', and barbus are all pointing to mistaken affinity and identity in French and English, the common name enteromis is proposed and used (see Discussion for more details).

3.6 | Enteromius cerinus sp. nov.

Figures 2b and 6b and Table 4.

Cheironym: *Enteromius* sp. 'angadiko 1'.

Common names:

French: enteromis jaune.

English: yellow enteromis.

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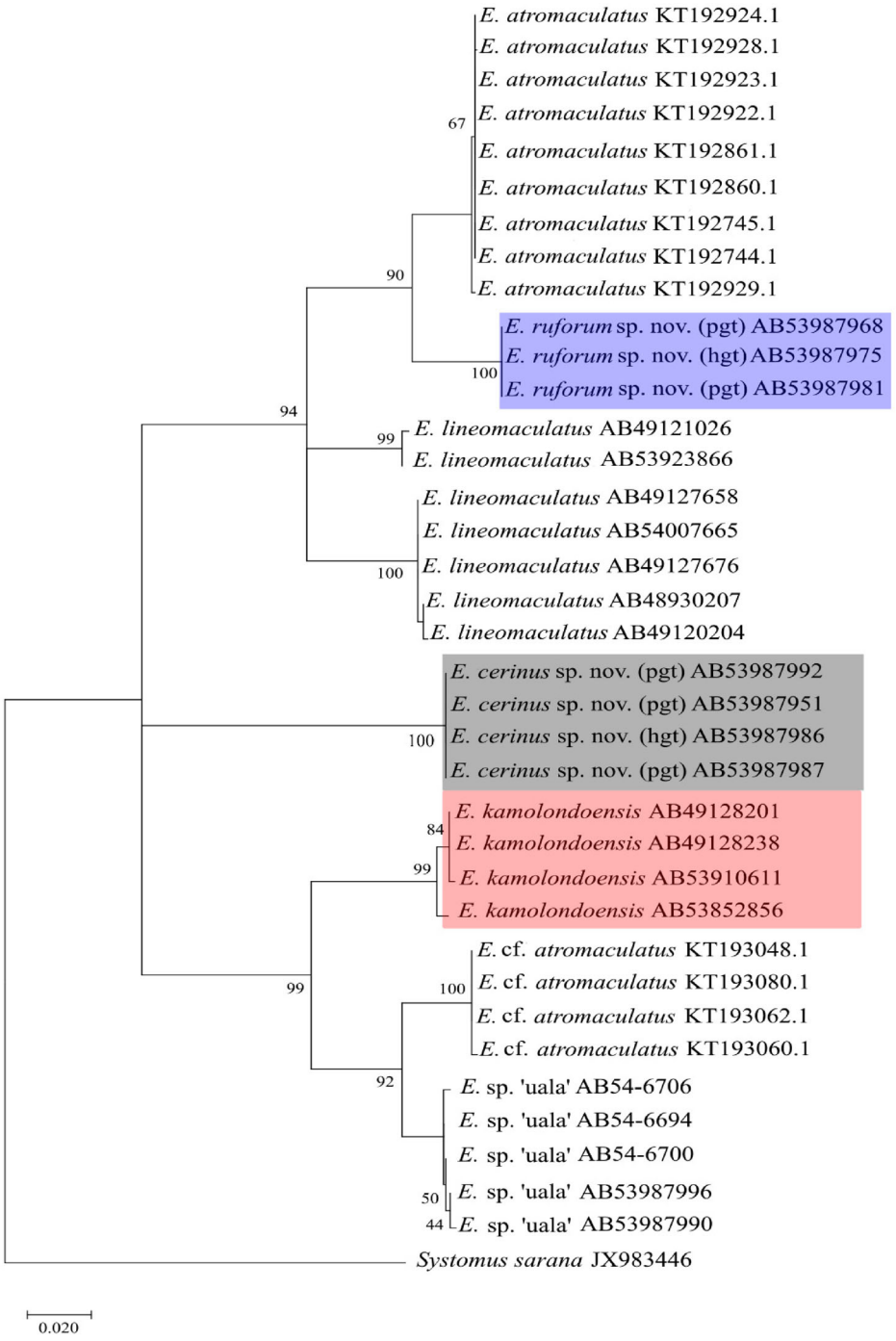


FIGURE 5 Maximum likelihood phylogenetic tree (8 species, 39 specimens) based on cytochrome oxidase subunit I (*COI*). Statistical node support (500 bootstrap replications) is illustrated. The position of both the (potentially) new species, *Enteromius* sp. 'angadiko 1' (=*Enteromius cerinus* sp. nov.), highlighted in grey, and *Enteromius* sp. 'angadiko 2' (=*Enteromius ruforum* sp. nov.), highlighted in blue. The scale bar refers to the branch lengths, measured in the number of substitutions per site. hgt, hologenetype; pgt, paragenetype.

Mamvu (i.e., a local central Sudanic language): ohitati madjali. Note that the general indiscriminate name for all members of the genus *Enteromius* is ohitati, which means fish from open or sunny areas. To make it specifically distinct from its congeners in the local Mamvu language, madjali, meaning yellow, has been added. As such, ohitati madjali refers to the general yellowish colour of the fish and literally means yellow ohitati.

3.6.1 | Holotype

RMCA 2019-019-P-0041, 43.0 mm *Ls*, DRC, Middle Congo, Angadiko River, upstream of Dingbo River bridge, Dingbo Village, 2°18′57.2″ N–28°45′0.5″ E, DNA tag: MRAC-RFO-009, collection OWR expedition, July 29, 2019.

3.6.2 | Paratypes

Same data as for holotype: AMNH 281166 (former RMCA 2019-019-P-0050-0051) (2), 38.3–44.5 mm *Ls*; BMNH 2024.5.28.1–2 (former RMCA 2019-019-P-0046-0047) (2), 45.1–46.4 mm *Ls*; CSB 2024_001_P_001_002 (former RMCA 2019-019-P-0048-0049) (2), 38.5–45.4 mm *Ls*; RMCA 2019-019-P-0054-0057 (4), 38.3–47.2 mm *Ls*; RMCA 2019-019-P-0042-0044 (3), 37.8–41.4 mm *Ls*, DNA tag:

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TABLE 3 Average genetic distance (GD in %) generated from the *COI* sequences between and within the set of selected *Enteromius* populations/species.

		Between groups								Within groups	
No.	Groups	1	2	3	4	5	6	7	8	K2P	un. p
1	*Enteromius atromaculatus*		**3.8**	5.3	6.0	**10.4**	10.5	10.7	9.5	0.1	0.1
2	*Enteromius* sp. 'angadiko 2'.	3.9		6.3	6.5	**9.5**	10.2	10.5	9.5	0.0	0.0
3	*Enteromius lineomaculatus* Rus	5.6	**6.7**		4.8	**10.6**	11.2	10.7	10.0	0.2	0.2
4	*E. lineomaculatus* Mal	6.4	**7.0**	5.0		**9.2**	10.3	9.6	9.6	0.0	0.0
5	*Enteromius* sp. 'angadiko 1'	11.4	**10.3**	11.6	10.0		9.5	10.0	9.9	0.0	0.0
6	*Enteromius kamolondoensis*	11.5	**11.2**	12.4	11.3	**10.3**		6.4	5.6	0.5	0.4
7	*E.* cf. *atromaculatus*	11.8	**11.6**	11.8	10.4	**10.9**	6.8		3.0	0.1	0.1
8	*Enteromius* sp. 'uala'	10.3	**10.4**	10.9	10.4	**10.7**	5.9	3.1		0.2	0.2

Note: K2P-distances and uncorrected p between species are separated by the diagonal, with uncorrected p (un. p) GDs given above and K2P GDs given below the diagonal, respectively. Bold values are between-group/species values for both the potentially new species: *Enteromius* sp. "angadiko 1' (= *Enteromius cerinus* sp. nov.) and *Enteromius* sp. 'angadiko 2' (= *Enteromius ruforum* sp. nov.).

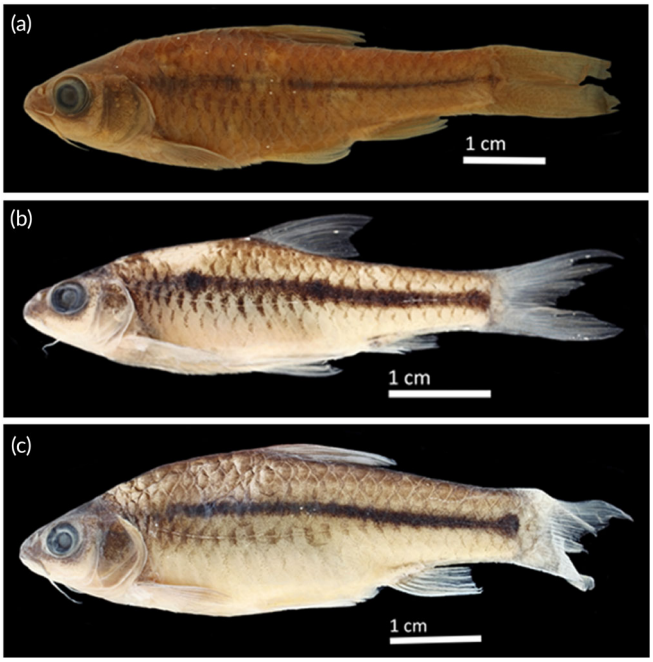


FIGURE 6 Photographs of the lateral view of a preserved specimens of: (a) *Enteromius kamolondoensis*, syntype, RMCA 122304, 50.7 mm L_S; (b) *Enteromius cerinus* sp. nov., holotype, RMCA 2019-019-P-0045, 46.8 mm L_S; and (c) *Enteromius ruforum* sp. nov., holotype, RMCA 2019-019-P-0073, 55.2 mm L_S.

MRAC-RFO-007-008-015; RMCA 2019-019-P-0045 (1), 39.1 mm *Ls*; RMCA 2019-019-P-0058-0059 (2), 39.3–45.1 mm *Ls*, DNA tag: MRAC-RFO-010-011; ZSM 49645 (former RMCA 2019-019-P-0052-0053) (2), 39.1–39.3 mm *Ls*.

Other locations: RMCA 2019-019-P-0060-0061 (2), 34.2–39.4 mm *Ls*, DRC, Middle Congo, Angadiko River, upstream of Dingbo River Bridge, Dingbo Village, 2°19′9.0″ N–28°44′56.2″ E, DNA tag: MRAC-RFO-034, -035, collection OWR expedition, July 30, 2019; RMCA 2019-019-P-0062 (1), 38.3 mm *Ls*, same data as RMCA 2019-019-P-0060-0061; RMCA 2019-019-P-0064-0067 (4), 39.8–45.3 mm *Ls*, DRC, Middle Congo, Angadiko River, downstream of Dingbo River Bridge, Dingbo Village, 2°18′35.5″ N–28°45′9.30″ E, collection OWR expedition, August 1, 2019.

3.6.3 | Diagnosis

Enteromius cerinus sp. nov. belongs to the group of species of *Enteromius* from the Congo basin *s.l.* for which the last unbranched dorsal-fin ray is flexible, simple, and not serrated along its posterior edge. First, *E. cerinus* sp. nov. can be easily distinguished from its congeners by the following unique combination of characters: two pairs of barbels [vs. no barbels in *Enteromius aspilus* (Boulenger 1907), *Enteromius baudoni* (Boulenger 1918), *Enteromius brazzai* (Pellegrin 1901), *Enteromius carens* (Boulenger 1912), *Enteromius erythrozonus* (Poll & Lambert 1959), *Enteromius haasianus* (David 1936), *E. jae* (Boulenger, 1903), *Enteromius toppini* (Boulenger, 1916), and *Enteromius trispilomimus* (Boulenger 1907); a single pair of barbels in *Enteromius brevidorsalis* (Boulenger 1915), *Enteromius candens* (Nichols & Griscom, 1917), *Enteromius hulstaerti* (Poll 1945), *Enteromius nigrifilis* (Nichols 1928), *Enteromius owenae* (Ricardo-Bertram 1943), *Enteromius papilio* (Banister & Bailey 1979), and *Enteromius syntrechalepis* (Fowler 1949)]; lateral line complete [vs. incomplete in *Enteromius brachygramma* (Boulenger 1915) and *Enteromius lujae* (Boulenger 1913)]; 10–11 circumpeduncular scales [vs. lower, 8 in *Enteromius lufukiensis* (Boulenger 1917), or higher, 17–18 in *Enteromius deguidei* (Matthes, 1964)]; 26–28 lateral line scales [vs. lower, 19–21 in *Enteromius okae* (Fowler 1949), 20–24 in *Enteromius stigmasemion* (Fowler, 1936), 21–22 in *Enteromius pygmaeus* (Poll & Gosse 1963), 22–25 in *Enteromius validus* (Stiassny, Liyandja & Monsembula Iyaba 2016), 23–25 in *Enteromius amanpoae* (Lambert, 1961), 23–26 in *Enteromius thespesios* Katemo Manda, Snoeks, Decru, Bills & Vreven 2020, 24 in *Enteromius stanleyi* (Poll & Gosse 1974), 24–25 in *Enteromius mediosquamatus* (Poll 1967), 25 in *Enteromius luluae* (Fowler 1930) and in *Enteromius tomiensis* (Fowler, 1936); or higher, 28–30 in *Enteromius*

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TABLE 4 Proportional measurements and meristics for *Enteromius cerinus* sp. nov., *Enteromius ruforum* sp. nov., and *Enteromius kamolondoensis*.

	Enteromius kamolondoensis			*Enteromius cerinus* sp. nov.			*Enteromius ruforum* sp. nov.		
Morphometrics	**Syntypes ($n = 6$)**	**Range ($n = 19$)**	**Mean**	**Holotype**	**Range ($n = 16$)**	**Mean**	**Holotype**	**Range ($n = 13$)**	**Mean**
Standard length (mm)	40.1–52.5	39.0–58.3	47.2	43	37.8–47.2	41.9	55.2	43.7–60.0	51.5
Body measurements (%L_S)									
Head length	26.2–27.6	26.2–28.6	27.5	26.1	24.8–27.3	26.1	27.4	25.4–27.9	26.7
Pre-dorsal distance	49.9–51.6	48.0–51.6	49.9	48.5	48.5–50.2	49.5	51.1	50.8–53.5	51.6
Dorsal-caudal distance	50.3–52.8	50.3–53.7	52.0	53.5	52.6–54.9	53.8	52.7	50.6–52.7	51.7
Post-dorsal distance	38.1–39.5	37.0–39.5	38.1	40.3	38.2–40.3	39.3	41.7	39.6–42.2	40.9
Dorsal-fin base length	13.8–15.0	13.8–15.6	14.5	15.6	14.9–16.2	15.7	13.8	13.7–15.2	14.5
Dorsal-fin length	24.3–26.4	24.3–26.5	25.6	26.7	25.4–27.6	26.7	25.9	24.3–27.7	25.9
Pre-pectoral distance	26.7–28.4	26.7–29.4	28.0	26.6	25.5–28.0	26.8	28.1	25.5–28.8	27.3
Pre-pelvic distance	50.7–52.5	49.3–52.5	50.9	49.1	47.9–51.6	50.0	52.0	50.0–52.9	51.6
Pre-anal distance	71.3–73.7	71.0–73.7	72.6	70.7	70.3–74.3	72.5	74.3	72.8–75.5	74.0
Anal-caudal distance	26.7–28.2	26.3–29.7	27.6	28.7	27.1–29.7	28.0	26.7	25.6–27.5	26.6
Post-anal distance	17.2–19.4	17.2–20.0	18.8	22.8	19.4–22.8	20.7	20.0	17.8–21.5	19.7
Minimum body depth	22.8–23.9	22.6–24.6	23.5	21.2	19.6–22.4	21.4	26.3	24.7–26.6	25.6
Maximum body depth	27.6–30.0	26.1–30.0	27.9	24.9	22.8–25.7	24.8	32.4	30.6–33.3	31.9
Maximum caudal- peduncle depth	15.0–16.2	13.7–16.6	15.3	15.1	13.2–15.1	14.3	17.2	16.1–17.9	17.2
Minimum caudal- peduncle depth	12.7–13.7	12.4–14.0	13.1	11.9	10.5–12.4	11.8	15.0	14.1–15.4	14.6
Head measurements (%L_H)									
Pre-occipital distance	71.4–73.3	70.9–73.3	72.2	80.0	79.1–80.9	79.9	72.1	71.1–73.4	72.5
Eye diameter	29.3–31.9	29.1–31.9	30.1	34.3	32.4–34.6	34.0	26.6	26.2–28.0	27.0
Snout length	28.0–30.1	27.9–30.1	29.0	32.8	31.7–34.6	32.8	31.1	30.4–33.2	31.2
Pre-operculum distance	67.1–69.6	66.7–69.6	68.1	71.0	70.1–73.3	71.7	70.2	69.9–72.2	70.7
Inter-orbital width	31.2–33.3	30.8–33.3	32.1	31.1	30.3–34.4	32.1	32.3	32.3–34.3	33.5
Anterior barbel length	23.6–27.2	23.6–27.2	25.0	34.3	32.2–35.3	33.8	27.0	24.7–27.9	26.4
Posterior barbel length	30.3–33.9	30.3–34.9	32.6	43.2	41.6–43.9	42.7	32.6	32.6–34.8	33.8
Meristic characters	**Sts**	**Range**	**Median**	**Ht**	**Range**	**Median**	**Ht**	**Range**	**Median**
Lateral line dorsal-fin origin scales	4.5	4.5	4.5	4.5	4.5	4.5	4.5	4.5	4.5
Lateral line pelvic-fin origin scales	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5
Lateral line anal-fin origin scales	2.5	2.5	2.5	2.5	2–2.5	2	2.5	2.5	2.5
Lateral line scales	27–29	27–30	28	26	26–28	27	24	24–26	25
Circumpeduncular scales	12	12	12	10	10–11	10	12	12	12
Pre-dorsal scales	10	10	10	10	9–10	10	9	9	9
Dorsal-fin rays	III 8	III 8	III 8	III 8	III 8	III 8	III 8	III 8	III 8
Anal-fin rays	III 5	III 5	III 5	III 5	III 5	III 5	III 5	III 5	III 5
Pectoral-fin rays	15	15–16	16	12	12–13	12	14	14–15	15
Pelvic-fin rays	8	8	8	8	8–9	9	8	8–9	9
Principal caudal-fin rays	19	19	19	19	19	19	19	19	19
Total number of vertebrae	28	28	28	27	27–28	28	26	26–27	27
Abdominal vertebrae	14	14	14	14	14	14	13	13	13

Note: The range (minimum–maximum) includes values for the holotypes and syntypes.
Abbreviations: Ht, holotype; Sts, syntypes.

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viviparus (Weber 1897), 28–32 in *Enteromius bifrenatus* (Fowler 1935), 29–32 in *Enteromius cercops* (Whitehead 1960), 29–33 in *E. innocens* (Pfeffer 1896), 30–32 in *E. lineomaculatus* (Boulenger, 1903), 30–33 in *Enteromius unitaeniatus* (Steindachner 1866), 31–33 in *Enteromius poechii* (Steindachner 1911), 32–33 in *Enteromius mocoensis* (Trewavas 1936), and 33–37 in *Enteromius motebensis* (Steindachner 1894)]; 4.5 scales between the dorsal-fin base and the lateral-line scales [vs. lower, 3.5 in *Enteromius ablabes* (Bleeker 1863), *Enteromius humeralis* (Boulenger 1902), *Enteromius macrops* (Boulenger, 1911), *Enteromius radiatus* (Peters 1853), and *Enteromius tshopoensis* (De Vos, 1991); or higher, 5.5 in *Enteromius marmoratus* (David & Poll, 1937)]; three black spots aligned on the flanks with a greyish-black midlateral band [vs. a midlateral band without black spots on the flanks in *Enteromius citrinus* (Boulenger 1920), *Enteromius lamani* (Lönnberg & Rendahl 1920), *Enteromius taeniopleura* (Boulenger 1917), and *Enteromius walshae* Mamonekene, Ibala Zamba & Stiassny 2018; 12–13 vertical blackish bars on flanks in *Enteromius fasciolatus* (Günther 1868); and a series of well-defined black spots without midlateral band on the flanks in *E. atromaculatus* (Nichols & Griscom, 1917), *Enteromius barotseensis* (Pellegrin 1920), *Enteromius camptacanthus* (Bleeker 1863), *Enteromius castrasibutum* (Fowler, 1936), *Enteromius caudosignatus* (Poll 1967), *Enteromius collarti* (Poll, 1945), *Enteromius lornae* (Ricardo-Bertram 1943), *Enteromius lukusiensis* (David & Poll, 1937), *Enteromius neefi* (Greenwood 1962), *Enteromius quadrilineatus* (David 1937), *Enteromius taeniurus* (Boulenger, 1903), *Enteromius tetrastigma* (Boulenger 1913), and *Enteromius urostigma* (Boulenger, 1917)]. Further, *E. cerinus* sp. nov. differs from the two most similar Congo basin species, that is, *E. kamolondoensis* and *E. ruforum* sp. nov. (described below), by a broad greyish-black midlateral band encompassing three black spots on the flanks (vs. a band without black spots on the flanks); lower number circumpeduncular scales, 10–11 (vs. 12, in both); lower maximum body depth, 22.8%–25.7% L_S (vs. 26.1%–30.0% and 30.6%–33.3%, respectively); and larger eye diameter, 32.4%–34.6% L_H (vs. 29.1%–31.9 and 26.2%–28.0%, respectively).

Finally, *E. cerinus* sp. nov. can also be distinguished from the six members of the same group known from the south-western part of the Nile basin and this by the following unique combination of characters: two pairs of barbels [vs. no barbels in *Enteromius anema* (Boulenger, 1903) and *Enteromius stigmatopygus* (Boulenger, 1903)]; 10–11 circumpeduncular scales [vs. lower, 8 in *Enteromius leonensis* (Boulenger 1915); or higher, 12–14 in *Enteromius perince* (Rüppell 1835)]; a broad greyish-black midlateral band encompassing three black spots on the flanks [vs. absence in *Enteromius alberti* (Poll 1939) and *Enteromius mimus* (Boulenger 1912)].

3.6.4 | Description

Based on the holotype and 15 paratypes. Proportional measurements and meristics characters of *E. cerinus* sp. nov. are given in Table 4. General lateral appearances in life and on a preserved specimen are shown in Figures 2b and 6b. Maximum observed size: 47.2 mm *L*s. Body fusiform. Dorsal profile from tip of snout to origin of dorsal fin slightly convex, slightly tapered to base caudal fin. Ventral profile from lower jaw to origin of posterior anal fin slightly convex, then slightly straight to caudal-fin base. Eye large and round situated laterally, straight interorbital profile. Snout rounded, mouth subterminal. Two pairs of barbels, anterior usually slightly shorter than posterior. Anterior barbel reaching up to three-quarters of eye, whereas posterior slightly exceeds posterior border of eye. Dorsal fin with III, 8 rays, distal margin slightly concave. Dorsal-fin origin slightly anterior to middle of body and anterior origin of pelvic fin. First branched dorsal-fin ray is longest, with posterior rays gradually decreasing in size. Pectoral fin with I, 11–12 rays, distal margin slightly convex, not reaching anterior base of pelvic fin. Anal fin with III, 5 rays, distal margin slightly concave, not reaching anterior base of caudal fin. Caudal fin forked with outer rays twice as long as median ones and both lobes rounded and of similar size. Complete lateral line (26–28 scales), slightly curved downward below the dorsal and becoming straighter behind dorsal- to caudal-fin base. Anus and genital opening situated immediately in front of anal-fin base.

3.6.5 | Colouration in life

Overall body colouration yellowish-brown, dorsally above midline with somewhat darker brown-coloured scale pockets forming small, vertical, brown bars (Figure 2b). Snout, upper jaw, and dorsal part of head also yellowish-brown. Sides, below lateral line, and lower half of head, that is, below the level of the eye, bright white with a metallic sheen. A broad greyish-black midlateral band of about a scale in height runs from tip of snout, over the operculum to the caudal-fin base, and encompassing three black spots. First spot is situated slightly in front the vertical of the dorsal-fin origin, the second one vertically to the last dorsal-fin ray, whereas the third one is situated toward the end of the caudal peduncle. All three black spots are sometimes veiled in live specimens and more visible in dead specimens (Figure S3). Another small spot is sometimes visible on the anterior base of the anal fin. The midlateral band is situated about half a scale height above the lateral line at the level of the anterior origin of the dorsal fin. This midlateral band with less-defined edges and surmounted by a narrow, silver-yellow, band reaching from upper end of operculum to the vertical of the last dorsal ray and sometimes to the center of caudal-fin base. A series of chevron-shaped markings along the scales of the lateral line reaching from the upper posterior end of operculum to the center of caudal-fin base. Caudal-fin base with a narrow, vertical, black band, more or less interrupted at level of lateral line. Operculum with a large black spot on upper half, resulting from the anterior extension of the greyish-black midlateral band, and bright white for its inferior part. Upper three-quarters of iris of eye greyish with a slight orange-reddish spot on superior quarter of iris. Lower quarter of iris bright white. Anterior and posterior barbels whitish. All fins whitish and transparent, except for (i) dorsal with yellowish rays on its proximal half, (ii) pectoral with black rays on its proximal half,

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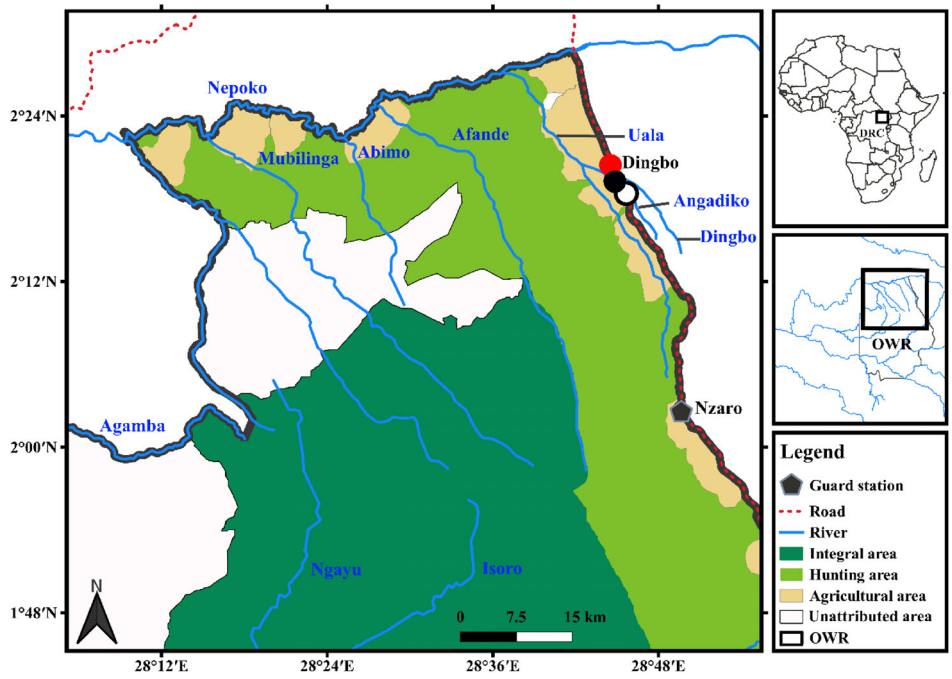


FIGURE 7 Distribution map for *Enteromius cerinus* sp. nov. and *Enteromius ruforum* sp. nov. in the Nepoko River subbasin draining the north part of the Okapi Wildlife Reserve (OWR) (Middle Congo, DRC). ●, type locality of *E. cerinus* sp. nov.; ○, type locality of *E. ruforum* sp. nov. Both species have the same site; thus, for a better visibility, both symbols are positioned next to each other; and ● and ⬟, respectively, Dingbo Village and Nzaro guard station, nearest to the type locality.



FIGURE 8 Main stream of the Angadiko River, near Dingbo Village, during the short dry season and type locality of *Enteromius cerinus* sp. nov. and *Enteromius ruforum* sp. nov. (July 30, 2019).

and (iii) caudal bright yellow, for its proximal two-thirds, except for the caudal rays themselves, which are white all over their entire length.

3.6.6 | Colouration of preserved specimens

Overall background colour of body greyish-brown above and whitish below midline and lateral line of body and head (Figure 6b). All yellowish-brown colouration above midline, on the caudal, and all other fins disappears. The same holds true for the narrow, silver-yellow band surmounting the greyish-black midlateral band. Nevertheless, the greyish-black midlateral band with the three encompassed black spots becoming more distinctly visible in some specimens. The small spot is sometimes visible on the anterior base of the anal fin. The small spot on the anterior base of the anal fin remains sometimes visible. The series of chevron-shaped markings along the scales of the lateral line persist from the upper end of operculum to the level of the caudal-fin base. Snout, upper jaw, and dorsal part of head greyish-brown. Black spot on operculum still present. However, pupil and iris, alike, (become) entirely black. All fins whitish. Anterior and posterior barbels still whitish.

3.6.7 | Distribution

Enteromius cerinus has only been found at the type locality, that is, Angadiko River, a left-bank affluent of the Dingbo River, the latter a right-bank affluent of the Uala River, which itself is a left-bank tributary of the Nepoko River near Dingbo Village in the north-eastern part of the OWR (Figure 7), and does, based on present collecting efforts, not appear to be widely distributed throughout the basin. During the main dry season (December to February), Angadiko River dries up completely, but no specimens have been found in other rivers in more downstream part of the basin, such as Dingbo or Uala. It was collected in calm waters during the minor dry season (June to August) because the river does not dry up completely during this season. Angadiko River is a small, shallow, forested river approximately 10 m wide, with an average depth of 0.5 to 1.0 m and running over a sandy silt bottom with mud (Figure 8). The average water temperature around 4:00 p.m. varied between 22.5 and 25.3°C (July 29, 2019).

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3.6.8 | IUCN conservation assessment proposition

Enteromius cerinus sp. nov. is endemic to the Angadiko River, a left-bank sub-affluent of the first order of the Nepoko River, draining the north-eastern part of the OWR (see Figure 7). This river is located in part of the OWR designated as an agricultural area (AA: see Introduction). In this area, human settlement is allowed. Resulting from the demographic growth, it is subject to increasing subsistence exploitation by human occupants. As a result, major threats were recorded during the collecting period (between 2019 and 2020) in the Uala River subbasin (see Section 4.4). Considering the very restricted distribution of the species, that is, the extent of occurrence (EOO) is less than 1 km^2 in the Uala River subbasin and the area of occupancy (AOO) is of 8 km^2. In addition, considering the gravity of the anthropogenic impacts in the (sub)basin, and the restricted AOO and number of locations, the species meets the requirements under criterion D (very small or restricted population) for Vulnerable (see IUCN Standards and Petitions Committee, 2024). Therefore, according to IUCN categories and criteria, *E. cerinus* sp. nov. should be considered as Vulnerable (VU) D2.

3.6.9 | Etymology

From the Greek *cerinus*, meaning waxy, wax coloured, yellowish, which refers to the yellowish colour of the dorsal part of the head, body, and the distal part of the two lobes of the caudal fin.

3.7 | Enteromius ruforum sp. nov.

Figures 1c and 6c and Table 4.

Cheironym: *Enteromius* sp. 'angadiko 2'.

Common name:

French: enteromis des Ruf.

English: Ruf's enteromis.

Mamvu: Ohitati ruf's, which literally means *Enteromius* of Ruf, that is, the couple Rosmarie Ruf and Karl Ruf to whom the species is dedicated (see Etymology below).

3.7.1 | Holotype

RMCA 2019-019-P-0073, 55.2 mm L_s, DRC, Middle Congo, Angadiko River, upstream of Dingbo River bridge, Dingbo Village, 2°18′57.2″ N–28°45′0.5″ E, DNA tag: MRAC-RFO-012, collection OWR expedition 2019, July 29, 2019.

3.7.2 | Paratypes

Same data as for holotype: AMNH 281167 (former RMCA 2019-019-P-0081) (1), 48.8 mm L_s; BMNH 2024.5.28.3 (former RMCA 2019-019-P-0079) (1) 49.8 mm L_s; CSB 2024_001_P_003 (former RMCA 2019-019-P-0080) (1), 60.0 mm L_s; RMCA 2019-019-P-0074-0075 (2), 48.7–53.0 mm L_s, DNA tag: MRAC-RFO-013-014; RMCA 2019-019-P-0076-0078 (3), 51.8–60.0 mm L_s; ZSM 49646 (former RMCA 2019-019-P-0082) (1), 51.8 mm L_s.

Other location: RMCA 2019-019-P-0083 (1), 48.8 mm L_s, DRC, Middle Congo, Angadiko River, upstream of Dingbo River bridge, Dingbo Village, 2°19′9.0″ N–28°44′56.2″ E, DNA tag: MRAC-RFO-036, collection OWR expedition 2019, July 29, 2019.

3.7.3 | Diagnosis

Enteromius ruforum sp. nov. belongs to the group of species of *Enteromius* from the Congo basin *s.l.* of which the last unbranched dorsal-fin ray is flexible, simple, and not serrated. First, *E. ruforum* sp. nov. can be easily distinguished from all other members of this group by the following unique combination of characters: two pairs of barbels (vs. no barbels in *E. aspilus*, *E. baudoni*, *E. brazzai*, *E. carens*, *E. erythrozonus*, *E. haasianus*, *E. jae*, *E. stigmatopygus*, *E. toppini*, and *E. trispilomimus*; or a single pair in *E. brevidorsalis*, *E. candens*, *E. hulstaerti*, *E. nigrifilis*, *E. owenae*, *E. papilio*, and *E. syntrechalepis*); lateral line complete (vs. lateral line incomplete in *E. brachygramma* and *E. lujae*); 12 circumpeduncular scales (vs. lower, 8 in *E. lufukiensis*, 8–10 in *E. amanpoae*, 10 in *E. humeralis*, *E. luluae*, and *E. mediosquamatus*, 11 in *E. lamani*; or higher, 17–18 in *E. deguidei*); 24–26 lateral line scales (vs. lower, 19–21 in *E. okae*, 20–22 in *E. stigmasemion*, 21–22 in *E. pygmaeus*; or higher, 27–30 in *E. taeniopleura*, 28 in *E. citrinus*, 28–30 in *E. viviparus*, 28–32 in *E. bifrenatus*, 30–32 in *E. lineomaculatus*, 30–33 in *E. unitaeniatus*, 31 in *E. innocens*, 31–33 in *E. poechii*, 32–33 in *E. mocoensis*, and 33–37 in *E. motebensis*); 4.5 lateral-line dorsal-fin origin scales (vs. 3.5 in *E. ablabes*, *E. macrops*, *E. radiatus*, and *E. tshopoensis*); absence of blackish vertical bars on flanks (vs. 12–13 blackish vertical bars on flanks in *E. fasciolatus*); blackish well-marked midlateral band on the flanks with a distinct black spot to the center of the caudal-fin base (vs. absence of midlateral band in *E. stanleyi*; a series of chevron-shaped markings along the lateral line in *E. thespesios*, *E. tomiensis*, and *E. validus*; and lateral band overlies a somewhat zigzag-patterned midlateral scale series in *E. walshae*); no spots on flanks (vs. well-defined spots on flanks in *E atromaculatus*, *E. barotseensis*, *E. camptacanthus*, *E. castrasibutum*, *E. caudosignatus*, *E. cercops*, *E. collarti*, *E. lornae*, *E. lukusiensis*, *E. marmoratus*, *E. neefi*, *E. quadrilineatus*, *E. taeniurus*, *E. tetrastigma*, and *E. urostigma*). Further, *E. ruforum* sp. nov. differs from the two most similar Congo basin species, that is, *E. cerinus* sp. nov. and *E. kamolondoensis* by a blackish, well-marked, midlateral band on the flanks, with a distinct black spot to the center of the caudal-fin base (vs. a greyish-black midlateral band encompassing three black spots on the flanks; and a greyish, midlateral band, generally less marked in its most anterior part, respectively), a high minimum body depth, 24.7%–26.6% L_S (vs. 19.6%–22.4% and 22.6%–24.6%, respectively); and a smaller eye diameter, 26.2%–28.0% L_H (vs. 32.4%–34.6% and 29.1%–31.9%, respectively).

Finally, *E. ruforum* sp. nov. can also be distinguished from the five species of the same group known from the south-western part of the Nile basin and this by the following unique combination of characters:

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two pairs of barbels (vs. no barbels in *E. anema*); 12 circumpeduncular scales (vs. 8 in *E. leonensis*); and a less broad, blackish, well-marked, midlateral band on the flanks, with a distinct black spot to the center of the caudal-fin base (vs. absent in *E. alberti* and *E. mimus* and with three small spots on the flanks in *E. perince*).

3.7.4 | Description

Based on the holotype and 12 paratypes. Proportional measurements and meristic characters of *E. ruforum* sp. nov. are given in Table 4. General appearance in life and on a preserved specimen is shown in Figures 2c and 6c. Maximum observed size 60 mm *Ls*. Body moderately high and fusiform. Dorsal profile from tip of snout to origin of dorsal fin slightly convex, slightly tapered to base of caudal fin. Ventral profile from lower jaw to origin of posterior anal fin slightly convex, then slightly concave to base of caudal fin. Eye large and round situated laterally, interorbital profile straight. Rounded snout, terminal mouth. Two pairs of barbels, anterior usually slightly shorter than posterior. Anterior barbel reaching up the center of eye, whereas posterior one up posterior border of eye. Dorsal fin with III, 8 rays. Distal margin of dorsal fin slightly concave. Dorsal-fin origin located at mid-body and slightly anterior (1 or 2 lateral-line scale(s)) to vertical through pelvic-fin insertion. First branched dorsal-fin ray longest, posterior rays gradually decreasing in size. Pectoral fin with I, 13–14 rays, distal margin with slightly convex, not reaching origin anterior of pelvic-fin base. Anal fin with III, 5 rays, distal margin with a slightly concave, not reaching origin anterior of caudal-fin base. Caudal fin forked with outer rays twice as long as median ones and both lobes rounded and of similar size. Complete lateral line (24–26 scales), slightly curved downward in front of the dorsal and becomes straighter behind the dorsal to the caudal-fin base. Anus and genital opening situated immediately in front of anal-fin base.

3.7.5 | Colouration in life

Overall body colouration dark brown-greenish, dorsally above midline with a metallic sheen on some of the scales (Figure 2c). Snout, upper jaw, and dorsal part of head dark brown-greenish as well. Instead, sides, below lateral line, and lower half of head, that is, below the level of the eye, white with a metallic sheen. A less broad, blackish, well-marked, midlateral band of about half a scale in height runs from the upper, posterior, end of the operculum to the center of the caudal-fin base, where it forms a distinct spot. Midlateral band situated about one scale in height above the lateral line at the level of the anterior origin of the dorsal fin. This midlateral band with well-defined edges and surmounted by a narrow, silver-yellow, band from behind the operculum to about midway the caudal peduncle. Caudal-fin base with a narrow, vertical, black band, more or less interrupted at level of lateral line. Operculum with a large black spot on its posterior upper half, whereas, instead, white for its inferior part. Upper three-quarters of iris of eye greyish with a slight orange-reddish spot on superior quarter of iris. Lower quarter of iris bright white. Anterior and posterior barbels greenish. All fins whitish and transparent with blackish rays on their proximal half, but for (i) the dorsal, (ii) the anal, and (iii) the caudal fin, light yellow toward their base.

3.7.6 | Colouration of preserved specimens

Overall background colour of body greyish-brown above and whitish below midline and lateral line of body and head (Figure 6c). All dark brown-greenish colouration with slight yellow on the flanks and head disappears. The same holds true for the narrow, silver-yellow band surmounting the greyish-black midlateral band. Nevertheless, the blackish midlateral band and the black spot on the center of the caudal-fin base, both persist well. Instead, a series of chevron-shaped markings sometimes present along the anterior-most base of the scales of the lateral line only poorly persist. Snout, upper jaw, and dorsal part of head also greyish-brown. Also, black spot on operculum still present. However, pupil and iris, alike, entirely black. All fins whitish. Anterior barbel greyish and posterior one whitish.

3.7.7 | Distribution

Enteromius ruforum has also only been found in its type locality, that is, Angadiko River, and does not appear widely distributed throughout the basin (Figure 7). It was collected in calm waters during the minor dry season (June to August) because the river does not dry up completely during this season (Figure 8) contrary to during the major dry season (December to February). For details, see under distribution heading of *E. cerinus*.

3.7.8 | IUCN conservation assessment proposition

Enteromius ruforum sp. nov. is endemic to the Angadiko River, a left-bank sub-affluent of the first order of the Nepoko River, draining the north-eastern part of the OWR (see Figure 7). This river is located in part of the OWR designated as an agricultural area (AA: see Introduction). In this area, human settlement is allowed. Resulting from the demographic growth, it is subject to increasing subsistence exploitation by human occupants. As a result, major threats were recorded during the collecting period (between 2019 and 2020) in the Uala River subbasin (see Discussion: anthropogenic threats). Considering the very restricted distribution of the species, that is, the EOO is less than 1 km^2 in the Uala River subbasin and the AOO is of 8 km^2. In addition, considering the gravity of the anthropogenic impacts in the (sub)basin, and the restricted AOO and number of locations, the species meets the requirements under criterion D (very small or restricted population) for Vulnerable (see IUCN Standards and Petitions Committee, 2024). Therefore, based on IUCN categories and criteria, *E. ruforum* sp. nov. should be considered as Vulnerable (VU) D2.

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3.7.9 | Etymology

Enteromius ruforum sp. nov. is dedicated to the couple Rosmarie Ruf and Karl Ruf (1950–2002†), in recognition of their vast, groundbreaking, and relentless engagement to protection and conservation issues in the region. Rosmarie Ruf is the actual director of the WCG at Epulu in the OWR. She has worked since 1987 in Epulu, even before the creation of the reserve, and has remained actively engaged in the service of nature protection in the OWR since. The late Karl Ruf, her husband, also worked for WCG in the OWR, but was unfortunately killed in a road accident while on a nature conservation mission.

3.8 | A first identification key to the *Enteromius* species of the OWR

1. Last unbranched dorsal-fin ray spinous, serrated.....**2**
Last unbranched dorsal-fin ray flexible, unserrated.....**5**
2. Lateral line incomplete, with only five to six anterior-most scales perforated.....*E.* cf. *apleurogramma*
Lateral line complete, all scales on lateral line perforated.....**3**
3. 28–30 lateral-line scales.....*E.* cf. *pellegrini*
26 or fewer lateral-line scales.....**4**
4. 21–23 lateral-line scales, with distinct black midlateral band on the flanks from the tip of the snout, through the eye, and reaching caudal-fin base.....*E. miolepis*
25–26 lateral-line scales; with black blotches on the flanks, these never forming a continuous midlateral band....*E. trinotatus*
5. Lateral line incomplete, that is, with only 2–6 anterior-most scales perforated, 8–10 circumpeduncular scales, 5–8 blackish vertical bars on the flanks.....*E. jae*
Lateral line complete, that is, all scales on lateral line perforated; 10–12 circumpeduncular scales; no blackish vertical bars on the flanks.....**6**
6. Inferior mouth; 10 circumpeduncular scales, presence of a black vertical bar behind operculum, and no spots along the flanks.....*E. humeralis*
Terminal mouth; 10–12 circumpeduncular scales; no black vertical bar behind operculum, but instead, eventually, with a series of distinct black spots on the flanks.....**7**
7. Presence of spots on the flanks.....**8**
Absence of spots on the flanks.....**9**
8. 10 circumpeduncular scales, 23 lateral line scales, a series of three distinct black spots on the flanks.....*E.* sp. '10 cps'
12 circumpeduncular scales, 25–26 lateral line scales, a series of 3–5 distinct black spots on the flanks.....*E. atromaculatus*
9. No midlateral band, marks or spots on the flanks.....*E.* cf. *brazzai*
With a well-marked midlateral band.....**10**
10. 10–11 circumpeduncular scales.....*E. cerinus* sp. nov.
12 circumpeduncular scales.....**11**
11. A blackish, well-marked, midlateral band along the flanks, distinct black spot on caudal-fin base.....*E. ruforum* sp. nov.
A greyish-black, less-marked, midlateral band along the flanks; no black spot on caudal-fin base.....*Enteromius* sp. 'uala'

4 | DISCUSSION

4.1 | Hidden species diversity in the *Enteromius* of the OWR

Recent studies using meristic, morphometric, and genetic DNA barcoding data have been carried out on the ichthyofauna of the northeastern part of the Congo basin, in general, and also on the *Enteromius* species from the region of the OWR, in particular. The results of these studies confirmed that the alpha-taxonomy of the *Enteromius* species in this region, the Aruwimi basin at large, is currently still insufficiently known (Decru et al., 2016; Van Ginneken et al., 2017). This is certainly due to the high species diversity, the high morphological similarity between species, and the large number of species new for science that this genus still contains (Lévêque, 1989a; Van Ginneken et al., 2017; Vreven et al., 2018).

Generally, the alpha-taxonomy of *Enteromius*, or the small African barbs, as previously referred to (see Skelton, 2016), is known to be difficult (Lévêque, 1989a; Van Ginneken et al., 2017). Several studies using molecular techniques, such as DNA barcoding, have certainly improved our scientific knowledge of this genus (Schmidt et al., 2017; Van Ginneken et al., 2017). Indeed, genetic tools have proven to be powerful for the identification of freshwater fish species in general (Becker et al., 2011; Pereira et al., 2013), but also to detect cryptic species diversity (Collins & Cruickshank, 2012; Decru et al., 2015; Goodier et al., 2011; Schmidt et al., 2017; Van Ginneken et al., 2017).

This is exemplified, first, by the description of new *Enteromius* species for science from all over the African continent, including *E. thespesios* from the Upper Lualaba basin [Upper Congo basin (DRC)] (Katemo Manda et al., 2020), and *Enteromius radari* from the Lowa basin [Upper Congo basin (DRC)] (Kisekelwa et al., 2022). Further, this is also exemplified by the revalidation of some other species, such as *E. tshopoensis* (De Vos 1991) from the Middle Congo basin (DRC) (Van Ginneken et al., 2017), *E. alberti* (Poll 1939) and *E. mimus* (Boulenger 1912) from the Lake Edward system (DRC, Uganda) (Maetens et al., 2020) and part of the Upper Nile basin. Both the two new species for science described in the present paper are only known from their shared type locality. As such, at least, further exploration of other tributaries of Nepoko basin (Middle Congo basin) will be critical to obtain a better view on their actual distribution and potentially additional hidden species diversity in the *Enteromius* genus of the subbasin.

The colour pattern and colouration of both the new species revealed to be very similar to *E. kamolondoensis* as characterised by the shared presence of a greyish-black midlateral band along the flanks, even if it differs between these species in some respect (see Figure 2 and Table 1). The presence of a blackish midlateral band is well known to occur in some *Enteromius* species presenting a thickened, that is, stout, and serrated last unbranched dorsal-fin ray, thus

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being a spine, such as in members of the *E. miolepis* group reported from the OWR (Kisekelwa et al., 2022; Van Ginneken et al., 2017). However, it has been far less reported from species presenting a flexible and unserrated last unbranched dorsal-fin ray, such as *E. kamolondoensis* and the two newly described species from the OWR.

In addition, a third (potential) new species, *Enteromius* sp. 'uala', with a flexible and unserrated last dorsal-fin ray and a greyish midlateral band has been identified from not only (i) the Uala River, a left-bank affluent of the Nepoko River in the OWR, but also (ii) the Tiyongo River, a small right-bank sub-affluent of the first order, of the Tshopo River, the latter a right-bank affluent of the upper stretch of the Middle Congo basin near Bafwakondima Village. Note that the Angadiko River, from which both new species are described in the present paper, is a left-bank sub-affluent of the Uala River. The (potentially) new species from the Uala River, however, has not been included here in the presented morphological approach, as its greyish midlateral band is not permanent. Instead, it is present in freshly caught specimens but quickly disappears after capture, giving way to a uniform silvery appearance on the flanks. This is also true for recently dead specimens. Nevertheless, this greyish midlateral band reappears in well-preserved specimens (see Figure S4). The disappearance of its greyish midlateral band might be explained by a reaction to the stress, suffered by the fish during capture, as observed in fish of other families, alike, such as Cichlidae and Salmonidae (see Border et al., 2018; Lehtonen et al., 2023; Lucena et al., 2022; Yi et al., 2021). Thus, to properly address this colour pattern identification problem, this (potentially) new species should be compared, in full detail, not only with (i) the most similar species with a midlateral band on the flanks, in life, but also with (ii) the most similar species lacking such band and thus possessing a uniform silvery appearance on the flanks. This will be done in a separate paper (Mayo Ilodiri et al., in preparation).

Often, when a (*Enteromius*) species is characterised by a clear specific colour pattern and occurs across a wide geographic range (species), identification problems are to be expected (Kisekelwa et al., 2022). Indeed, the disappearance of the black midlateral band has also been observed in specimens identified *E.* cf. *miolepis*, a species for which the last unbranched dorsal-fin ray is thickened, that is, stout, and serrated, from the Nyabingula River, a right-bank affluent of the Lowa basin (Upper Congo basin: DRC) (Kisekelwa et al., 2020). As such, this colour pattern phenomenon seems to be more widespread as occurring in both morphological *Enteromius* groups, that is, not only in those where the last unbranched dorsal-fin ray is flexible and unserrated but also in those where the last unbranched dorsal-fin ray is thickened and serrated.

To date, nine *Enteromius* species are known from the rivers draining the OWR (Decru et al., 2017; Van Ginneken et al., 2017). Within the framework of the present study, new field expeditions were organised (2019–2020), especially in the rivers draining the north-eastern part of the reserve. Based on these new collections, two new *Enteromius* species for science are herein described from one of those river basins, that is, the Nepoko. In addition, one more (potentially) new species, here referred to as *Enteromius* sp. 'uala', is also reported from that basin. This last one remains, nevertheless, still to be formally described (see above). This brings the number of known species of *Enteromius* from the reserve to a total of 11 + 1, which increases the number of species by 25% (i.e., 18% for the two added ones for a total of 11 species), and this only by collecting in previously unexplored affluent rivers draining the reserve. However, several other affluents on the left bank of the Nepoko River north of the reserve, from up- to downstream, including the Afande, Abimo, and Mubilinga (see Figure 7), remain unexplored to the present day, and thus might (still) hold more undocumented *Enteromius* species diversity.

4.2 | A new overarching English and French common name for the species of the genus *Enteromius* Cope, 1867: Enteromis

Most of the species that are currently referred to as members of the genus *Enteromius*, containing diploid African small cyprinids (Agnèse et al., 1990; Berrebi et al., 1990, 1996; Golubtsov & Krysanov, 1993; Ráb et al., 1994), have in the past been considered part of the genus *Barbus* Daudin 1805, currently known to be only composed of tetraploid European and (Western) Asian cyprinids (Ráb & Collares-Pereira, 1995). As a result, in the past too, they have often been referred to, in English common language, as small barbs (see Lévêque, 2003; De Weirdt et al., 2007) and, similarly, as 'petits barbeaux' or 'petits *Barbus*' in French common language (see Lévêque, 2003; De Weirdt et al., 2007).

This is also true for the Congo basin *s.l.* However, both French and English are colonial languages in the sense that they have foreign origin for most of the people actually living in the Congo basin *s.l.* and, thus, were introduced with the arrival of the colonists. This means that for most people currently living in the Congo basin *s.l.* neither language is their mother tongue (Maalu-Bungi et al., 2008). Furthermore, most fish species are invisible to most of these persons. This is especially true for those who know both languages and who mostly reside in or near (large) cities. Thus, considering the reality of their alienation from this aquatic fish fauna, most of the Congo basin *s.l.* species still do not have a common name in both introduced common languages. Therefore, regarding the Congo basin *s.l.*, both French and English have mostly been used in a scientific context, strictly or more broadly, even when referring collectively to *Enteromius* species as 'petit barbeaux' (French) or (small) barbs (English) in the past. Indeed, as a result, the so-called common names, in both languages, are in fact not so commonly used.

Furthermore, although both genera, that is, *Barbus* and *Enteromius*, belong to the family Cyprinidae, based on current molecular evidence, *Barbus* species are part of the subfamily Barbinae, whereas, instead, *Enteromius* species are part of the tribe Smiliogastrini (Yang et al., 2015: Figure 2d; Table 3). Despite their very distinct affinities, the introduction of this new generic name was not without some controversy, particularly because it was considered that "(…) "the poor resolution provides no support" for revalidation of the generic name

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Enteromius to accommodate all African diploid "*Barbus*" (…)" (see Schmidt & Bart Jr., 2015 in Skelton, 2016: 346), as part of the species currently included in the genus may still need reattribution to other genera in the future (Hayes & Armbruster, 2017; Schmidt & Bart Jr., 2015; Skelton, 2016; Stiassny et al., 2016; Stiassny & Sakharova, 2016). As such, their past common appellation as small barbs is, at least, also confusing. In the same sense, they have sometimes also been referred to as minnows in English common language (see Katemo Manda et al., 2020; Kisekelwa et al., 2022; Skelton, 2001). However, this appellation refers, first, to members of the genus *Phoxinus* Rafinesque 1820, which is part of the family Leuciscidae, and known from northern and Central Europe. In addition, it refers to members of a diverse assemblage of other genera, such as *Pimephales* Rafinesque 1820 (Leuciscidae), and even families, such as Cyprinodontidae with *Cyprinodon* Lacépède 1803, which are both American genera and, as such, are also not closely related to *Enteromius*. In the same line of thought, therefore, this common language appellation is also suboptimal.

However, the importance of linking up the scientific naming, particularly for species new to science, with the local common name(s) of these species is crucial in the context of the major anthropogenic impacts to which this fauna is nowadays subjected. Indeed, in this context, effective communication on the diversity of hidden and little-known species is essential. This is illustrated in the present paper by the discovery of two new species for science. Both lack a common species-specific name in the two common language fields, that is, native (Mamvu) and foreign (English and French). Indeed, in our case, in the local language Mamvu, there is only a 'generic'/group name and thus no proper name for each of both individual species.

Thus, an extended (for Mamvu) and new (for English and French) common names are here proposed. These names are specifically designed for popularization by providing a nomenclature more accessible for non-professionals, but which mirrors the scientific system and its underlying concepts (see Shaw, 2016: 172). This is especially true for the two new species described in the present paper and considering the importance of providing local language tools to communicate the critical message of hidden and unknown species diversity. In this very specific context, learned names (sensu Shaw, 2016: 173) are proposed, which consist of two elements: (i) a group name, corresponding here to their common local 'generic' name in Mamvu or referring to their current scientific generic name (for English and French), and (ii) a modifier, here making an explicit and obvious link, for both, to their scientific species name.

Therefore, indeed, within this context also, we are of the opinion that it is wise to present a new, overarching, common English (and French) name for the members of the genus *Enteromius*, which we here like to refer to as enteromis. In classical Latin *Barbus* species were already referred to as barbus (or barbel), a fish with sensitive whisker-like projections round its mouth (Ayto, 2005). Thus, it is their common Latin appellation that has subsequently become barbs, in common English, and barbeaux, in common French. In the same line of thought, enteromis for *Enteromius* becomes a common appellation derived from its Greek scientific name, which is a contraction of the Greek enteron (intestine) and myo, mys (muscle) (Cope, 1867; Romero, 2002 as cited in Froese & Pauly, 2024). Nevertheless, we are fully aware that due to the paraphyly of what is currently referred to as *Enteromius* (Hayes & Armbruster, 2017: figure 2; Skelton, 2016; Yang et al., 2015: figure 2), not all species, most likely, will remain part of that lineage and thus keep *Enteromius* as their scientific generic name and its derived common name. However, as for those new local names proposed, we see no major problems as they are composed of a group name and a modifier, if needed, changing the first will suffice. Indeed, this will result in a change in the English and French common names. Nevertheless, such changes do not, in our opinion, present a major problem considering that there is no major historical affinity between the local Congo basin *s.l.* people, with the proposed English and French common names. This is, however, very different for some long-standing common names in other parts of Africa.

Hence, our suggestion does not imply that all common names should be changed in this way. For instance, southern Africa, and South Africa in particular, has a relatively long history (since 1822, see Skelton, 2001: vii) of local/vernacular names in Afrikaans, which are better retained. However, at least in the Congo basin *s.l.*, in the context of *Enteromius*, where there is neither such a historical language issue in English nor in French, our suggestion seems justified. As noted by Skelton (2001: 62), from a scientific point of view, common names should be standardised. Nevertheless, even in southern Africa, common names have changed when a need arose (Skelton, 2002: 172–173). For instance, common name of some *Labeobarbus* species were changed to better mediate the message of distinct species by adding a geographic component to otherwise identical names, that is, yellowfish. For us the widespread heritage of the common names barb (in English) and 'petit barbeau' (in French) mainly reflects a recent colonial history, with little local application beyond a scientific framework. This is in some ways also true for southern Africa, where a learned name composed of 'ghieliemientjie', in Afrikaans, the language of the colonials who settled in the region, with a specifier, has been proposed and used for many species (see Skelton, 2001; Van der Waal & Skelton, 1984). In addition, let us not forget that although widespread in southern Africa, as for many other colonial languages in other African countries, Afrikaans is also a colonial language. However, at a common generic level, the locally widespread appellation barb or minnow is and has also been used (see Skelton, 2001). Nevertheless, a new postcolonial message about biodiversity heritage can also be mediated with this proposed new overarching common designation, namely that Africa has its own lineage of small-sized, in this case diploid, cyprinids, which are not at all barbs nor minnow but enteromis, instead. This seems even more true when considering the patchwork of English and French as official and/or spoken (colonial) languages over the African continent.

Furthermore, in general, different human populations use different local, common, or vernacular names for the same biological species (Jernudd & Thuan, 1984), that is, the species diversity reality that is out there. As such, even in the same common language often different local names might be given to the same species depending, for instance, on the language dialect or the distinct (hydro)geographical

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FIGURE 9 Anthropogenic threat occurring in the Okapi Wildlife Reserve (OWR) and specifically one most affecting its aquatic habitats and ichthyofauna in the north-eastern of the protected area (PA): An abandoned artisanal fishing dam on the main channel of the Angadiko River (Mbisa Congo II; August 1, 2019) (2°18′57.2″ N–28°45′0.5″ E at 847 m altitude).

region where it is spoken. However, uniform and correct vernacular names are important to communicate (Jernudd & Thuan, 1984), such as in our present case of two unknown *Enteromius* species, the message of (scientifically) hidden, unknown, and unique species diversity. This is true even if both these species have, based on our present knowledge, no direct human economic, but only some subsistence, value, indeed. As such, a vernacular name should not only be presented in English and/or French but also in the locally spoken language(s) to enable a relational sharing of the reality of the humanly unrecognised and unique species diversity found in the rivers out there. This will also help in communicating the message of the need for local protection and conservation (Díaz-Restrepo et al., 2022; Jemmett et al., 2022; Silvano et al., 2022). Binomial scientific names are not really appropriate to communicate on this kind of species diversity issues with a non-scientific audience as, instead, it creates distance and thus the feeling of alienation, non-concern, and non-comprehension.

4.3 | The Angadiko: A temporary river

Temporary, or intermittent, rivers are natural ecosystems drying out into pools or, in some cases, completely during dry periods, resulting in an alternance of wet and dry areas and periods of the river over the annual cycle (Acuña et al., 2014; Costigan et al., 2017; Datry et al., 2014; Jaeger et al., 2017; Larned et al., 2010; Steward et al., 2012). These kinds of rivers are typical of hydro-climate regimes as found in the Californian (northern America), Mediterranean (southern Europe), and South African regions (Allen et al., 2017; Kerezsy et al., 2017; Larned et al., 2010; Quiñones & Moyle, 2015; Tooth, 2000). However, they are also found in Central Eastern, Northern, and Western Africa (Sahel region) (Kerezsy et al., 2017; Messager et al., 2021). Nevertheless, to our knowledge, no temporary rivers are reported for the small affluent rivers of the Congo basin (Runge, 2007; Messager et al., 2021).

Moreover, for Africa, few studies on the ecology of the fishes eventually surviving in those pools are available. This is true for the Limpopo River (South Africa: van der Waal, 1997), the Mzingwane River (Zimbabwe: Minshull, 2008), and streams flowing into Lake Kariba and affluents of the middle Zambezi River basin itself (Zimbabwe: Kadye & Chakona, 2012; Strauch et al., 2015). These are all located in semi-arid or low rainfall areas (<500 mm; Kerezsy et al., 2017). Regularly associated with these temporary rivers are some African extremophile fishes, which present adaptations to desiccation, that is, Protopteridae (lungfishes), Clariidae (air-breathing catfishes), Anabantidae (climbing gouramies), and Nothobranchiidae (African rivulines). The first three families are air breathing and present different types of adapted breathing organs to this effect (Kerezsy et al., 2017; Lévêque & Paugy, 2017). Instead, Nothobranchiidae presents a short life span and eggs buried in diapause in the dry bottom substrate to survive total desiccation (Reichard, 2015). Other fish species, that is, Cyprinidae, are able to perform migrations to recolonise these temporal upstream habitats (Kerezsy et al., 2017). To our knowledge, however, no studies including temporary rivers are known for the Congo basin, situated for a large part as for the rivers draining the OWR, in the tropical forest area of Central Africa.

Dry areas along temporary rivers can either create a patchwork of disconnected pools, if groundwater levels are sufficient or present a natural long stretch of totally dry riverbed (Costigan et al., 2017; Pires et al., 2010; Quiñones & Moyle, 2015). Small rivers in drier African areas are strongly seasonal and dry out completely every year (Kerezsy et al., 2017; Marshall et al., 2017). For these small rivers, recolonization after flow resumption will depend on the number of potential fish settlers residing in downstream parts of the basin (Marshall et al., 2017; Pires et al., 2010, 2014). In larger temporary rivers, however, the dispersal rate of fish survivors, housed in persistent pools during the dry season, and/or their mobility are fundamental (Gratwicke & Marshall, 2005; Kerezsy et al., 2017; Minshull, 2008; Pires et al., 2010, 2014; Pires & Magalhães, 2013).

The OWR is situated in an area with humid long-term average groundwater recharge (see MacDonald et al., 2021: figures 1 and 2). However, even though the Angadiko River itself remains present a few pools during the minor dry season (June to August), it seems to dry out completely during the major dry season (December to February) (W.M.I., personal observations from July to October, 2019–2020). As such, the Angadiko River is presenting either edaphic (no superficial and subsuperficial water) or hyporheic (no superficial water, but with subsuperficial water) aquatic state (see Gallart et al., 2012 for complete definition; Bonada et al., 2020: figure 1). During the periods when the water level is lowering in the rivers, that is, toward the start of the major dry season (December to February) and the minor dry season (June to August), fish thus tend to move downstream toward the larger, perennial rivers. However, this is also

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when ecopage fishery is practiced, a fishing practice using dam building to cross the main channel of these affluent rivers (Figure 9). In the region and for these affluents, to increase fish catch, the ecopage fishery is most often combined with the use of ichthyotoxic plants (see below).

After the major dry season (December to February), the fish diversity occurring in the Angadiko River is fully dependent on the species occurring downstream, in the main channel of the Dingbo River. Upstream migration, however, is potentially limited by anthropogenic constructions, that is, fishing dams for ecopage fishery (see Section 4.4 for details), during the attempted recolonization with flow resumption in the rainy season (Kukuła & Bylak, 2022).

This alternation of wet and dry periods in temporary rivers is a natural process. However, it could lead to long-lasting drought periods, with drought conditions becoming increasingly severe following the current trends in the climatic change (Costigan et al., 2017; Kerezsy et al., 2017). Therefore, further studies are needed to (i) assess which aquatic state, that is, edaphic, hyporheic, based on their geomorphology structure, the rivers concerned present; (ii) confirm or refute that upstream pools are present in the Angadiko River; and (iii) investigate the ecology of the fishes living in those affluent river systems.

4.4 | Anthropogenic threats and protection needs

Both the new *Enteromius* species, described in the present paper, were collected from the Angadiko River, which is located close to the human habitations of Dingbo Village (Figure 7). This river is located in part of the OWR designated as an agricultural area (AA: see Introduction) and is thus subject to increasing subsistence exploitation by its human occupants as a result of its demographic growth. As such, both these new species are subject to intensifying anthropogenic impacts such as the destruction of habitats by agriculture practices along rivers and the intensive use of ecopage fishery as a fishing method. Further, to be more efficient, this fishing technique using artisanal dam building is most often combined with the use of ichthyotoxic plants, such as *Tephrosia vogelii* Hook.f. (Fabaceae) and *Millettia duchesnei* De Wild. (Fabaceae), as fish poison (W.M.I., personal observations 2019–2020). However, these barriers can easily be removed, and fish migration and assemblages can thus be rehabilitated (Kukuła & Bylak, 2022), with long-term effects, thus, being minimal.

What, instead, can be done regarding the use of the ichthyotoxic plants? *Tephrosia vogelii* is widely used by the human inhabitants of the OWR as an ichthyotoxin for fishing. It is also used, as such, in the Uala basin (W.M.I., personal communication, 2019–2020). However, except for scientific purposes, this in accordance with the derogation as stipulated in the law of the DRC (see above: Section 2), the use of ichthyotoxins is forbidden. The same holds true for the pollution of waters with toxic wastes, chemical substances, pollutants, and any other dangerous products; this is in accordance with article 73 of the law of February 11, 2014 on nature conservation in the DRC. This prohibition is also reiterated in the directives of access to natural resources/riches of the OWR (Ohole & Ntumba, 2017). Nevertheless, as an ichthyotoxin, *T. vogelii* is often planted in the home gardens, which are to be found in the OWR behind the habitations toward the forest (W.M.I., personal observations 2019–2020). As such, we like to propose that the woody herbs that are *T. vogelii* be removed from these home gardens, that is, destroyed.

Indeed, naturally, *T. vogelii* occurs in fallows and secondary formations (Flora of Central Africa, 2023). As such, as the OWR is covered by primary forest in the Uala River basin region, *Tephrosia* is not part of its natural flora. Therefore, it appears to be planted around villages for its use as an ichthyotoxin. Thus, *T. vogelii* cultures around the villages could be destroyed as to discourage its further use. In addition, *T. vogelii* has been classified Least Concern (LC) based on its global IUCN red list evaluation (BGCI, 2019). This further supports that its removal and extirpation around the villages from the OWR can be carried out without major danger with regard to its survival as a species.

Another plant locally used as an ichthyotoxin is the large native Congo basin forest liana, *Millettia duchesnei* (Ngandeu et al., 2008: 258). The species has, to date, not been evaluated (NE) for the IUCN red list (see IUCN, 2023). As such, not much is known about the anthropogenic threats it is subjected to. However, it seems to be quite abundant in the forest of the Uala River basin, as fishers easily found it along the river banks of the region (W.M.I., personal observations 2019–2020). Members of the genus *Millettia*, and *M. duchesnei* itself, have been reported with regard to their/its use as a fish poison and insecticide and the genus and *M. duchesnei* (Turumbu people, living in the Tshopo province), both, are known for their local medicinal application, of which at least part of it has been confirmed by modern pharmacological research (Banzouzi et al., 2008: 214; Jena et al., 2020; Ngandeu et al., 2008).

As such, regulations regarding the mandatory removal of the ecopage dams after use and of *Tephrosia* from the home gardens and other locations, in the OWR, should be established. Furthermore, the prohibited use of ichthyotoxins, as inscribed in DRC law (see above), should be implemented. These guidelines will be essential for the long-term survival of both species, as well as, at least, for all fish cohabiting in these very specific temporary river habitats. As such, it is hoped that the discovery of both the new species will draw greater attention to the critical importance of freshwater fish protection in rivers draining the OWR, in particular, and beyond, the Congo basin as a whole. Finally, we also hope that this message will reach not only more conservationists responsible for the OWR, as one of the numerous PAs in the DRC, but also, more broadly, all those responsible for conservation and protection of aquatic diversity of the Congo basin, in general.

5 | COMPARATIVE MATERIAL EXAMINED

5.1 | Enteromius kamolondoensis

All from the Democratic Republic of the Congo: RMCA 49598–609 (3 of 12 syntypes), 50.2–52.5 mm *Ls*; RMCA 49610–2020 (3 of

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11 syntypes), 40.1–51.3 mm *Ls*, Upper Congo, Bukama, channels of Lake Kasibasiba; RMCA 122304–306 (2 of 3), 39–50.7 mm *Ls*, Manono; RMCA 122307–308, 55.8–57.2 mm *Ls*; RMCA 82159–162, 42.9–51.5 mm *Ls*, Manono Marshes; RMCA 51252–261 (5 of 10), 39.5–48.6 mm *Ls*, Kikondja, Luvoi River.

AUTHOR CONTRIBUTIONS

Wilson Mayo Ilodiri was responsible for the fieldwork, fish identification, study design, and data analyses and wrote the first versions of the manuscript. Taylor Mambo Baba and Célestin Danadu Mizani were responsible for fieldwork and preliminary fish identification and critically reviewed the last version of the manuscript. Charlotte E.T. Huyghe was mainly responsible for the molecular work, sequence data analyses, and writing and co-supervision of the paragraphs related to this part of the paper. Luis M. da Costa contributed to the final writing and editing of the manuscript. Charlotte E.T. Huyghe and Luis M. da Costa made an equal contribution to this work. Emmanuel J.W.M.N. Vreven supervised the research, final fish identification, study design, data analyses and critically reviewed all versions of the manuscript. All authors discussed, read, and rewrote portions of the manuscript and approved its final version.

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REFERENCES

Abell, R., Thieme, M. L., Revenga, C., Bryer, M., Kottelat, M., Bogutskaya, N., Coad, B., Mandrak, N., Contreras Balderas, S., Bussing, W., Stiassny, M. L. J., Skelton, P., Allen, G. R., Unmack, P., Naseka, A., Ng, R., Sindorf, N., Robertson, J., Armijo, E., … Petry, P. (2008). Freshwater ecoregions of the world: A new map of biogeographic units for freshwater biodiversity conservation. *Bioscience*, *58*, 403–414.

Acuña, V., Datry, T., Marshall, J., Barceló, D., Dahm, C. N., Ginebreda, A., McGregor, G., Sabater, S., Tockner, K., & Palmer, M. A. (2014). Why should we care about temporary waterways? *Science*, *343*(6175), 1080–1081. https://doi.org/10.1126/science.1246666

Agnèse, J. F., Berrebi, P., Lévêque, C., & Guégan, J. F. (1990). Two lineages, diploid and tetraploid, demonstrated in African species *Barbus* (Osteichthyes, Cyprinidae). *Aquatic Living Resources*, *3*, 305–311.

Akaike, H. (1974). A new look at statistical model identification. *Tree Transaction on Automatic Control*, *19*, 716–723.

Allen, M. G., Beatty, S. J., & Morgan, D. L. (2017). Aquatic fauna refuges in Margaret river and the cape to cape region of Australia's

10958649, 2025, 2, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/jfb.15883 by John Carroll University, Wiley Online Library on [18/10/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Mediterranean-climatic Southwestern Province. *FiSHMED Fishes in Mediterranean Environments*, *2017*(2), 26p. https://doi.org/10.29094/FiSHMED.2017.002

Armstrong, R. A. (2014). When to use the Bonferroni correction. *Ophthalmic Physiological Optics*, *34*, 502–508.

Ayto, J. (2005). *Word origins–The hidden histories of English words from A to Z*. A & C Black.

Bamba, M., Vreven, E. J., & Snoeks, J. (2011). Description of *Barbus teugelsi* sp. nov. (Cypriniformes: Cyprinidae) from the little Scarcies basin in Guinea. *Africa. Zootaxa*, *2998*, 48–65.

Banzouzi, J. T., Prost, A., Rajemiarimiraho, M., & Ongoka, P. (2008). Traditonal uses of the African *Millettia* species (Fabaceae). *International Journal of Botany*, *4*(4), 406–420.

Becker, S., Hanner, R. H., & Steinke, D. (2011). Five years of FISH-BOL: Brief status report. *Mitochondrial DNA*, *22*, 3–9. https://doi.org/10.3109/19401736.2010.535528

Bektas, Y., Aksu, I., Kaya, C., & Turan, D. (2018). DNA barcoding of the genus *Capoeta* (Actinopterygii: Cyprinidae) from Anatolia. *Turkish Journal of Fisheries and Aquatic Sciences*, *19*, 739–752. https://doi.org/10.4194/1303-2712-v19_9_03

Berra, T. M. (2007). *Freshwater fish distribution* (p. 645). Academic Press.

Berrebi, P., Kottelat, M., Skelton, P., & Ráb, P. (1996). Systematics of *Barbus*: State of the art and heuristic comments. *Folia Zoologica*, *45*(Suppl. 1), 5–12.

Berrebi, P., Lévêque, C., Cattaneo-Berrebi, G., Agnèse, J. F., Guégan, J. F., & Machordom, A. (1990). Diploid and tetraploid African *Barbus* (Osteichthyes, Cyprinidae): On the coding of differential gene expression. *Aquatic Living Resources*, *3*(4), 313–323. https://doi.org/10.1051/alr:1990032

BGCI. (2019). Botanic gardens Conservation International (BGCI) & IUCN SSC global tree specialist group. 2019. *Tephrosia vogelii. The IUCN red list of threatened species* 2019: E.T146197294A146197296. Available at: https://doi.org/10.2305/IUCN.UK.2019-2.RLTS.T146197294A146197296.en (accessed: October 2023)

Bonada, N., Cañedo-Argüelles, M., Gallart, F., von Schiller, D., Fortuño, P., Latron, J., Llorens, P., Múrria, C., Soria, M., Vinyoles, D., & Cid, N. (2020). Conservation and Management of Isolated Pools in temporary rivers. *Water*, *12*(10), 2870. https://doi.org/10.3390/w12102870

Bookstein, F., Chernoff, B., Elder, R., Humphries, J., Smith, G., & Strauss, R. (1985). Morphometrics in evolutionary biology. *Academy of Natural Sciences of Philadelphia Special Publication*, *15*, 1–277.

Border, S. E., Piefke, T. J., Fialkowski, R. J., Tryc, M. R., Funnell, T. R., DeOliveira, G. M., & Dijkstra, P. D. (2018). Color change and pigmentation in a color polymorphic cichlid fish. *Hydrobiologia*, *832*, 175–191. https://doi.org/10.1007/s10750-018-3755-0

Boulenger, G. A. (1903). Diagnoses of four new species of *Barbus* from the Nile. *Annals and Magazine of Natural History (Series 7)*, *12*(71), 532–533.

Boulenger, G. A. (1911). Catalogue of the freshwater fishes of Africa. In *British museum (natural history)* (Vol. 2, p. 529). American Killifish Association.

Boulenger, G. A. (1916). *Catalogue of the fresh-water fishes of Africa in the British museum (natural history). London, Catalogue of the Fresh-Water Fishes of Africa in the British Museum (Natural History)* (pp. 1–392). Taylor and Francis.

Bruslé, S., & Quinard, J. (2001). *Biologie des poissons d'eau douce européens* (p. 256p). Lavoisier.

Chakrabarty, P. (2010). Genetypes: A concept to help integrate molecular phylogenetics and taxonomy. *Zootaxa*, *2632*, 67–68.

Collins, R. A., & Cruickshank, R. H. (2012). The seven deadly sins of DNA barcoding. *Molecular Ecology Resources*, *13*, 969–975. https://doi.org/10.1111/1755-0998.12046

Cope, E. D. (1867). Supplement on some new species of American and African fishes. *Transactions of the American Philosophical Society (New Series)*, *13*(3), 400–407.

Costigan, K. H., Kennard, M. J., Leigh, C., Sauquet, E., Datry, T., & Boulton, A. J. (2017). Flow regimes in intermittent rivers and ephemeral streams. In T. Datry, N. Bonada, & A. Boulton (Eds.), *Intermittent Rivers and ephemeral streams* (pp. 51–78) Chapter 2.2. Academic Press.

Datry, T., Larned, S. T., & Tockner, K. (2014). Intermittent rivers: A challenge for freshwater ecology. *Bioscience*, *64*(3), 229–235. https://doi.org/10.1093/biosci/bit027

Daudin, F. M. (1805). *Barbus*. In *Dictionnaire des sciences naturelles*, *BAN—BLU* (p. 58). Tome quatrième. Paris (Levrault, Schoell & Cie.) [Série 1] v. 4: 1-483. Dictionnaire des sciences Naturelles [Série 1] Vol. **4**. [Year also given as 'An XIII' of the French revolutionary calendar].

David, L., & Poll, M. (1937). Contribution à la faune ichthyologique du Congo Belge: Collections du Dr. H. Schouteden (1924-1926) et d'autres récolteurs. *Annales du Musée du Congo Belge*, *3*, 189–294.

De Vos, L. (1990). *Données préliminaires sur l'ichtyofaune de l'Epulu dans le futur Parc National de la forêt de l'Ituri (Zaïre)* (p. 31). Rapport non publié, UNIKIS.

De Vos, L. (1991). Description de *Barbus tshopoensis* sp. nov. du bassin du Zaïre (Pisces, Cyprinidae). *Journal of African Zoology*, *105*, 97–103.

De Vos, L., & Snoeks, J. (1994). The non-cichlid fishes of Lake Tanganyika. *Archiv für Hydrobiologie*, *44*, 391–405.

De Weirdt, D., Getahun, A., Tshibwabwa, S., & Teugels, G. G. (2007). Cyprinidae. In M. L. J. Stiassny, G. G. Teugels, & C. D. Hopkins (Eds.), *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, pp. 466–572). Paris, France: Institut de recherche pour le développement and Muséum National d'Histoire Naturelle; Tervuren, Belgium: Musée Royal de l'Afrique Centrale.

Decru, E., Moelants, T., De Gelas, K., Vreven, E., Verheyen, E., & Snoeks, J. (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 Ecology Resources*, *16*, 342–352.

Decru, E., Snoeks, J., & Vreven, E. (2015). A taxonomic evaluation of the *Hepsetus* from The Congo Basin with the revalidation of *H. Microlepis* (Teleostei: Hepsetidae). *Ichthyological Exploration of Freshwaters*, *26*(3), 273–287.

Decru, E., Vranken, N., Bragança, P. H. N., Snoeks, J., & Van Steenberge, M. (2019). Where ichthyofaunal provinces meet: The fish fauna of the Lake Edward system East Africa. *Journal of Biology of Fishes*, *96*(5), 1186–1201. https://doi.org/10.1111/jfb.13992

Decru, E., Vreven, E., Danadu, M., Walanga, A., Mambo, T., & Snoeks, J. (2017). Ichthyofauna of the Itimbiri, Aruwimi and Lindi/Tshopo rivers (Congo Basin): Diversity and distribution patterns. *Acta Ichthyologica & Piscatorial*, *47*, 225–247.

Díaz-Restrepo, A., Balcombe, K., Fraser, I., Smith, R. J., & Veríssimo, D. (2022). Testing branding techniques on species common names to improve their fundraising profile for conservation. *Animal Conservation*, *25*(1), 27–37. https://doi.org/10.1111/acv.12715

Dumont, H. J. (2009). The Nile. Origin, environment, limnology and human use. *Monographiae Biologicae*, *89*, 4–648.

Flora of Central Africa. (2023). *Tephrosia vogelii* Hook.f. Available at: https://www.floredafriquecentrale.be/species/S562389

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 of Philadelphia*, *88*, 243–335.

Fricke, R., Eschmeyer, W. N., & Van der Laan, R. (2024). Eschmeyer's catalog of fishes: Genera. Species. http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp (accessed: April 18, 2024)

Froese, R., & Pauly, D. (2024). FishBase. World wide web electronic publication. Available at www.fishbase.org, version (02/2024). https://www.fishbase.org/search.php

Gallart, F., Prat, N., García-Roger, E. M., Latron, J., Rieradevall, M., Llorens, P., Barberá, G. G., Brito, D., De Girolamo, A. M., Lo Porto, A., Buffagni, A., Erba, S., Neves, R., Nikolaidis, N. P., Perrin, J. L.,

10958649, 2025, 2, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/jfb.15883 by John Carroll University, Wiley Online Library on [18/10/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Querner, E. P., Quiñonero, J. M., Tournoud, M. G., Tzoraki, O., … Froebrich, J. (2012). A novel approach to analysing the regimes of temporary streams in relation to their controls on the composition and structure of aquatic biota. *Hydrology and Earth System Sciences*, *16*(9), 3165–3182. https://doi.org/10.5194/hess-16-3165-2012

Golubtsov, A. S., & Krysanov, E. Y. (1993). Karyological study of some cyprinid species from Ethiopia. The ploidy differences between large and small *Barbus* of Africa. *Journal of Fish Biology*, *42*(3), 445–455. https://doi.org/10.1111/j.1095-8649.1993.tb00347.x

Goodier, S. A. M., Cotterill, F. P. D., O'Ryan, C., Skelton, P. H., & de Wit, M. J. (2011). Cryptic diversity of African Tigerfish (genus *Hydrocynus*) reveals palaeogeographic signatures of linked Neogene geotectonic events. *PLoS One*, *6*, e28875. https://doi.org/10.1371/journal.pone.0028775

Gratwicke, B., & Marshall, B. E. (2005). Fish migrations in two seasonal streams in Zimbabwe African. *Journal of Aquatic Science*, *30*(2), 107–118. https://doi.org/10.2989/16085910509503844

Hammer, Ø., Harper, D. A., & Ryan, P. D. (2001). PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica*, *4*(1), 9.

Hayes, M. M., & Armbruster, J. W. (2017). The taxonomy and relationships of the African small barbs (Cypriniformes: Cyprinidae). *Copeia*, *105*, 348–362. https://doi.org/10.1643/CI-15-348

ICAR World Bank Report. (2013). Nile Basin initiative for the Nile equatorial lakes subsidiary action program (NELSAP) regional agricultural trade and productivity project (phase II). Report No: IRC 2447.

IUCN. (2023). The IUCN red list of threatened species. Version 2022-2. https://www.iucnredlist.org https://www.iucnredlist.org/fr/search/list?useTrades=6&searchType=species

IUCN Standards and Petitions Committee. (2024). Guidelines for using the IUCN red list categories and criteria: Version 16. Prepared by the Standards and Petitions Committee. https://www.iucnredlist.org/documents/RedListGuidelines.pdf

IUCN/WCMC. (1995). *Désignation pour la liste du Patrimoine Mondial Réserve de Faune à Okapis (RD Congo)*. IUCN/WCMC.

Ivanova, N. V., Zemlak, T. S., Hanner, R. H., & Hebert, P. D. (2007). Universal primer cocktails for fish DNA barcoding. *Molecular Ecology Notes*, *7*, 544–548. https://doi.org/10.1111/j.1471-8286.2007.01748.x

Jaeger, K. L., Sutfin, N. A., Tooth, S., Michaelides, K., & Singer, M. (2017). Geomorphology and sediment regimes of intermittent rivers and ephemeral streams. In T. Datry, N. Bonada, & A. Boulton (Eds.), *Intermittent rivers and ephemeral streams* (pp. 21–49) Chapter 2.1. Academic Press.

Jemmett, A. M., Groombridge, J. J., Hare, J., Yadamsuren, A., Burger, P. A., & Ewen, J. G. (2022). What's in a name? Common name misuse potentially confounds the conservation of the wild camel *Camelus ferus*. *Oryx*, *57*(2), 175–179. https://doi.org/10.1017/S0030605322000114

Jena, R., Rath, D., Rout, S. S., & Kar, D. M. (2020). A review on genus *Millettia*: Traditional uses, phytochemicals and pharmacological activities. *Saudi Pharmaceutical Journal*, *28*(12), 1686–1703. https://doi.org/10.1016/j.jsps.2020.10.015

Jernudd, B. H., & Thuan, E. (1984). Naming fish: A problem exploration. *Language in Society*, *13*(2), 235–244. https://doi.org/10.1017/S0047404500010393

Kadye, W. T., & Chakona, A. (2012). Spatial and temporal variation of fish assemblage in two intermittent streams in north-western Zimbabwe. *African Journal of Ecology*, *50*(4), 428–438. https://doi.org/10.1111/j.1365-2028.2012.01338.x

Kashindye, B. B., Katemo Manda, B., Friel, J. P., Chakona, A., & Vreven, E. (2021). *Chiloglanis msirii*, a new species of African suckermouth catfish (Teleostei: Mochokidae), from the upper Congo Basin. *Ichthyological Exploration of Freshwaters*, *31*, 33–46.

Katemo Manda, B., Snoeks, J., Chocha Manda, A., & Vreven, E. (2021). *Nannocharax hadros* (Teleostei: Distichodontidae), a new species from the Kalule Nord river in the Upemba National Park, upper Congo Basin. *Ichthyological Exploration of Freshwaters*, *30*, 317–330.

Katemo Manda, B., Snoeks, J., Decru, E., Bills, R., & Vreven, E. (2020). *Enteromius thespesios* (Teleostei: Cyprinidae): A new minnow species with a remarkable sexual dimorphism from the south-eastern part of the upper Congo river. *Journal of Fish Biology*, *96*(5), 1160–1175. https://doi.org/10.1111/jfb.14108

Katemo Manda, B., Snoeks, J., Decru, E., Brecko, J., & Vreven, E. (2023). Revision of *Nannocharax luapulae* Boulenger, 1915 (Characiformes: Distichodontidae) from the upper Congo Basin: Evidence for a species pair. *Journal of Fish Biology*, *103*(3), 557–573. https://doi.org/10.1111/jfb.15400

Kerezsy, A., Gido, K., Magalhães, M. F., & Skelton, P. H. (2017). The biota of intermittent rivers and ephemeral streams: Fishes. In T. Datry, N. Bonada, & A. Boulton (Eds.), *Intermittent Rivers and ephemeral streams* (pp. 273–298) Chapter 4.5. Academic Press.

Kimura, M. (1980). A simple method for estimating evolutionary rate of base substitutions through comparative studies of nucleotide sequences. *Journal of Molecular Evolution*, *16*, 111–120. https://doi.org/10.1007/BF01731581

Kisekelwa, T., Snoeks, J., Decru, E., Schedel, F. B. D., Isumbisho, M., & Vreven, E. (2022). A mismatch between morphological and molecular data in lineages of *Enteromius* (Cypriniformes: Cyprinidae) from the Lowa Basin (East Democratic Republic of the Congo: DRC) with the description of a new species. *Systematics and Biodiversity*, *20*(1), 2135630. https://doi.org/10.1080/14772000.2022.2135630

Kisekelwa, T., Snoeks, J., & Vreven, E. (2020). An annotated checklist of the fish fauna of the river systems draining the Kahuzi-Biega National Park (upper Congo: Eastern DR Congo). *Journal of Fish Biology*, *96*(3), 700–721. https://doi.org/10.1111/jfb.14264

Kukuła, K., & Bylak, A. (2022). Barrier removal and dynamics of intermittent stream habitat regulate persistence and structure of fish community. *Scientific Reports*, *12*, 1512. https://doi.org/10.1038/s41598-022-05636-7

Kumar, S., Stecher, G., & Tamura, K. (2016). MEGA7: Molecular evolutionary genetics analysis version 7.0 for bigger datasets. *Molecular Biology and Evolution*, *33*, 1870–1874. https://doi.org/10.1093/molbev/msw054

Lambert, J. G. (1961). Contribution à l'étude des poissons de forêt de la cuvette congolaise. *Annales du Musée Royal de l'Afrique Centrale*, *93*, 7–40.

Larned, S. T., Datry, T., Arscott, D. B., & Tockner, K. (2010). Emerging concepts in temporary-river ecology. *Freshwater Biology*, *55*, 717–738. https://doi.org/10.1111/j.1365-2427.2009.02322.x

Lehtonen, T. K., Candolin, U., & Wong, B. B. M. (2023). Environmental variation promotes colour morph-specific behavioural differences in a cichlid fish. *Animal Behaviour*, *197*, 123–130. https://doi.org/10.1016/j.anbehav.2023.01.005

Lévêque, C. (1989a). Remarques taxinomiques sur quelques petits *Barbus* (Pisces, Cyprinidae) d'Afrique de l'Ouest (première partie). *Cybium*, *13*(2), 165–180. https://doi.org/10.26028/cybium/1989-132-005

Lévêque, C. (1989b). Remarques taxinomiques sur quelques petits *Barbus* (Pisces, Cyprinidae) d'Afrique de l'Ouest (deuxième partie). *Cybium*, *13*(3), 197–212. https://doi.org/10.26028/cybium/1989-133-001

Lévêque, C. (2003). Cyprinidae. In D. Paugy, C. Lévêque, & G. G. Teugels (Eds.), *The fresh and brackish water fishes of West Africa* (Vol. 1. Coll. Faune et flore tropicales. Institut de recherche de dévelopement; Muséum national d'histoire naturelle, and Tervuren, Musée royal de l'Afrique Centrale, pp. 323–436).

Lévêque, C., & Daget, J. (1984). Cyprinidae. In J. Daget, J. P. Gosse, & D. F. E. Thys van den Audenaerde (Eds.), *Check-list of the freshwater fishes of Africa/catalogue des poisons d'eau douce d'Afrique* (Vol. 1, pp. 217–342). CLOFFA.

Lévêque, C., & Paugy, D. (2017). Diversity of responses to environmental constraints and extreme environmental conditions. In D. Paugy, C.

10958649, 2025, 2, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/jfb.15883 by John Carroll University, Wiley Online Library on [18/10/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Lévêque, & O. Otero (Eds.), *The inland water fishes of Africa – Diversity, ecology and human use* (pp. 259–268). IRD Éditions & RMCA.

Levin, B. A., Simonov, E., Matveyev, M. P., Artaev, O. N., Mustafayev, N. J., Pashkov, A. N., & Roubenyan, H. R. (2018). DNA barcoding of the fishes of the genus *Alburnoides* (Actinopterygii, Cyprinidae) from Caucasus. *Mitochondrial DNA*, *29*(1), 49–55. https://doi.org/10.1080/24701394.2016.1238900

Liyandja, T. L. D., Armbruster, J. W., Poopola, M. O., & Stiassny, M. L. J. (2022). Evolutionary convergence in body shape obscures taxonomic diversity in species of the African *Labeo forskalii* group: Case study of *L. parvus* Boulenger 1902 and *L. ogunensis* Boulenger 1910. *Journal of Fish Biology*, *101*(4), 898–913. https://doi.org/10.1111/jfb.15148

Lucena, C. A. S. d., Kullander, S., Norén, M., & Calegari, B. (2022). Conjectures and refutations: Species diversity and phylogeny of *Australoheros* from coastal rivers of southern South America (Teleostei: Cichlidae). *PLoS One*, *17*(12), e0261027. https://doi.org/10.1371/journal.pone.0261027

Maalu-Bungi, C., Mutombo, H. M., Mbula, P., Motingea, M. A., Makokila, N., Mundeke, O., Donzo, B., & Nsenga, I. M. (2008). *Atlas Linguistique de l'Afrique centrale–Situation linguistique en Afrique centrale-La République Démocratique du Congo. Nouvelle édition revue et corrigée*. CERDOTOLA.

MacDonald, A. M., Lark, R. M., Taylor, R. G., Abiye, T., Fallas, H. C., Favreau, G., Goni, I. B., Kebede, S., Scanlon, B., Sorensen, J. P. R., Tijani, M., Upton, K. A., & West, C. (2021). Mapping groundwater recharge in Africa from ground observations and implications for water security. *Environmental Research Letters*, *16*(3), 034012. https://doi.org/10.1088/1748-9326/abd661

Maetens, H., Van Steenberge, M., Snoeks, J., & Decru, E. (2020). Revalidation of *Enteromius alberti* and presence of *Enteromius* cf. *mimus* (Cypriniformes: Cyprinidae) in the Lake Edward system East Africa. *European Journal of Taxonomy*, *700*, 1–28. https://doi.org/10.5852/ejt.2020.700

Marshall, B., Chakona, A., Tweddle, D., Skelton, P., Bills, R., & Minshull, J. (2017). The composition and health of fishes in residual dry season habitats in southern Africa (Strauch *et al*. 2015). *Marine and Freshwater Research*, *68*(2), 203–206. https://doi.org/10.1071/MF15295

Matthes, H. (1964). Les poisons du Lac Tumba et de la région d'Ikela, études systématiques et zoogéographique. *Annales du Musée Royale de l'Afrique central*. *Bruxelles*, *126*, 1–198.

Messager, M. L., Lehner, B., Cockburn, C., Lamouroux, N., Pella, H., Snelder, T., Tockner, K., Trautmann, T., Watt, C., & Datry, T. (2021). Global prevalence of non-perennial rivers and streams. *Nature*, *594*, 391–397. https://doi.org/10.1038/s41586-021-03565-5

Minshull, J. L. (2008). Dry season fish survival in isolated pools and within sand-beds in the Mzingwane river, Zimbabwe. *African Journal of Aquatic Science*, *33*(1), 95–98. https://doi.org/10.2989/AJAS.2007.33.1.13.397

Neumann, D., Obermaier, H., & Moritz, T. (2016). Annotated checklist for fihes of the Main Nile Basin in The Sudan and Egypt based on recent specimen records (2006-2015). *Cybium*, *40*(4), 287–317. https://doi.org/10.26028/cybium/2016-404-004

Ngandeu, F., Bezabih, M., Ngamga, D., Tchinda, A. T., Ngadjui, B. T., Abegaz, B. M., Dufat, H., & Tillequin, F. (2008). Rotenoid derivatives and other constituents of the twigs of *Millettia duchesnei*. *Phytochemistry*, *69*(1), 258–263.

Nichols, J. T., & Griscom, L. (1917). Fresh-water fishes of the Congo Basin obtained by the American museum Congo expedition, 1909-1915. *Bulletin of the American Museum of Natural History*, *37*, 653–756. http://hdl.handle.net/2246/1069

Oellermann, L. K., & Skelton, P. H. (1990). Hexaploidy in yellowfish species (Barbus, Pisces, Cyprinidae) from southern Africa. *Journal of Fish Biology*, *37*(1), 105–115. https://doi.org/10.1111/j.1095-8649.1990.tb05932.x

Ohole, N. A., & Ntumba, K. B. (2017). *Directives d'Accès aux Ressources Naturelles dans la Reserve de Faune à Okapis*. Epulu.

Pereira, L. H. G., Hanner, R., Foresti, F., & Oliveira, C. (2013). Can DNA barcoding accurately discriminate megadiverse neotropical freshwater fish fauna? *BMC Genetics*, *14*, 20. https://doi.org/10.1186/1471-2156-14-20

Pires, D. F., Beja, P., & Magalhães, M. F. (2014). Out of pools: Movement patterns of Mediterranean stream fish in relation to dry season refugia. *River Research and Applications*, *30*(10), 1269–1280. https://doi.org/10.1002/rra.2776

Pires, D. F., & Magalhães, M. F. (2013). First data on the movements of *Iberochondrostoma almacai* (Coelho, Mesquita & Collares-Pereira, 2005) out of dry-season pools in a Mediterranean stream. *Anales de Biologia*, *35*, 85–87. https://doi.org/10.6018/analesbio.0.35.12

Pires, D. F., Pires, A. M., Collares-Pereira, M. J., & Magalhães, M. F. (2010). Variation in fish assemblages across dry season pools in a Mediterranean stream: Effects of pool morphology, physicochemical factors and spatial context. *Ecology of Freshwater Fish*, *19*(1), 74–86. https://doi.org/10.1111/j.1600-0633.2009.00391.x

Poll, M. (1938). Poisson du Katanga (Bassin du Congo) récoltés par le professeur Paul Brien. *Revue de Zoologie et de Botanique Africaines*, *30*(4), 389–423.

Poll, M. (1976). *Exploration du Parc National de l'Upemba: mission G. F. de Witte (1946-1949)* (p. 73). Fondation pour favoriser les recherches scientifiques en Afrique.

Quiñones, R. M., & Moyle, P. B. (2015). California's freshwater fishes: Status and management. *FiSHMED Fishes in Mediterranean Environments*, *2015*(1), 20p. https://doi.org/10.29094/FiSHMED.2015.001

Ráb, P., & Collares-Pereira, M. J. (1995). Chromosomes of European cyprinid fishes (Cyprinidae, Cypriniformes): A review. *Folia Zoologica*, *44*(3), 193–214.

Ráb, P., Machordom, A., Perdices, A., & Guegan, J. F. (1994). Karyotypes of three «small» *Barbus* species (Cyprinidae) from Republic of Guinea (Western Africa) with a review on karyology of African small *Barbus*. *Caryologia*, *48*(3–4), 299–307. https://doi.org/10.1080/00087114.1995.10797339

Rafinesque, C. S. (1820). Fishes of the Ohio river. [Ichthyologia Ohiensis, Part 5]. *Western Review and Miscellaneous Magazine*, *2*(4), 235–242.

Reichard, M. (2015). The evolutionary ecology of African annual fishes. In N. Berois, G. García, & R. De Sá (Eds.), *Annual fishes: Life history strategy, diversity, and evolution* (pp. 133–158). CRC Press.

Ren, Q., & Mayden, R. L. (2016). Molecular phylogeny and biogeography of African diploid barbs, '*Barbus*', and allies in Africa and Asia (Teleostei: Cypriniformes). *Zoologica Scripta*, *45*(6), 642–649. https://doi.org/10.1111/zsc.12177

RFO. (2004). Zonage et conservation dans le Nord-est de la RDC: le cas de la Réserve de Faune à Okapis (RFO). Report.

Rice, W. R. (1989). Analyzing tables of statistical tests. *Evolution*, *43*(1), 223–225. https://doi.org/10.1111/j.1558-5646.1989.tb04220.x

Runge, J. (2007). The Congo River, Central Africa. In A. Gupta (Ed.), *Large Rivers: Geomorphology and management* (pp. 293–309). John Wiley & Sons Ltd.

Schmidt, R. C., & Bart, H. L., Jr. (2015). Nomenclatural changes should not be based on equivocally supported phylogenies: Reply to Yang et al. 2015. *Molecular Phylogenetics and Evolution*, *90*, 193–194. https://doi.org/10.1016/j.ympev.2015.05.025

Schmidt, R. C., Bart, H. L., Jr., & Nyingi, W. D. (2017). Multi-locus phylogeny reveals instances of mitochondrial introgression and unrecognized diversity in Kenyan barbs (Cyprininae: Smiliogastrini). *Molecular Phylogenetics and Evolution*, *111*, 35–43. https://doi.org/10.1016/j.ympev.2017.03.015

Shaw, P. A. (2016). Three types of zoological common names and their formation-processes. *Nordic Journal of English Studies*, *15*, 171–187. https://doi.org/10.35360/njes.369

Silvano, R. A. M., Pereyra, P. E. R., Begossi, A., & Hallwass, G. (2022). Which fish is this? Fishers know more than 100 fish species in

10958649, 2025, 2, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/jfb.15883 by John Carroll University, Wiley Online Library on [18/10/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

megadiverse tropical rivers. *Facets*, *7*, 988–1007. https://doi.org/10.1139/facets-2021-0136

Skelton, P. H. (2001). *A complete guide to the freshwater fishes of southern Africa*. Struik Publishers.

Skelton, P. H. (2002). Changes to the scientific and common names of southern African freshwater fishes. *African Journal of Aquatic Science*, *27*(2), 171–174. https://doi.org/10.2989/16085914.2002.9626588

Skelton, P. H. (2016). Name changes and additions to the southern African freshwater fish fauna. *African Journal of Aquatic Science*, *41*(3), 345–351. https://doi.org/10.2989/16085914.2016.1186004

Snoeks, J. (2000). How well known is the ichthyodiversity of the ancient African lakes? In a. Rossiter & H. Kawanabe (eds), *ancient lakes: Biodiversity, ecology and evolution*. *Advances in Ecological Research*, *31*, 17–38.

Somers, K. M. (1986). Multivariate allometry and removal of size with principal components analysis. *Systematic Biology*, *35*(3), 359–368. https://doi.org/10.1093/sysbio/35.3.359

Srivathsan, A., & Meier, R. (2012). On the inappropriate use of Kimura-2-parameter (K2P) divergences in the DNA-barcoding literature. *Cladistics*, *28*(2), 190–194. https://doi.org/10.1111/j.1096-0031.2011.00370.x

Steward, A. L., von Schiller, D., Tockner, K., Marshall, J. C., & Bunn, S. E. (2012). When the river runs dry: Human and ecological values of dry riverbeds. *Frontiers in Ecology and the Environment*, *10*(4), 202–209. https://doi.org/10.1890/110136

Stiassny, M. L. J., Liyandja, T. L. D., & Monsembula Iyaba, R. J. C. (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. https://doi.org/10.1206/3848.1

Stiassny, M. L. J., & Sakharova, H. (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. https://doi.org/10.1111/jfb.12901

Strauch, A. M., Kapust, A. R., & Jost, C. C. (2015). Composition and health of fish in refugia habitat of ephemeral tributaries to the lower Zambezi in southern Africa. *Marine and Freshwater Research*, *66*(4), 343–351. https://doi.org/10.1071/MF14100

Tamura, K., Stecher, G., & Kumar, S. (2021). MEGA11: Molecular evolutionary genetics analysis version 11. *Molecular Biology and Evolution*, *38*(7), 3022–3027. https://doi.org/10.1093/molbev/msab120

Thieme, M. L., Abell, R., Stiassny, M. L. J., Skelton, P., Lehner, B., Teugels, G. G., Dinerstein, E., Toham, A. K., Burgess, N., & Olson, D. (2005). *Freshwater ecoregions of Africa and Madagascar: A conservation assessment*. Island Press.

Tooth, S. (2000). Process, form and change in dryland rivers: A review of recent research. *Earth-Science Reviews*, *51*(1–4), 67–107. https://doi.org/10.1016/S0012-8252(00)00014-3

UNESCO. (2010). *Le patrimoine mondial dans le bassin du Congo*. UNESCO, Paris. Report, 63 pp.

USBGN. (1964). *Republic of the Congo (Léopoldville): Official standard names approved by the United States board on geographic names* (p. 80). Office of Geography.

Van der Waal, B. C. W. (1997). Some observations on the fish life in a seasonal sand river. *Southern African Journal of Aquatic Science*, *23*(1), 95–102. https://doi.org/10.1080/10183469.1997.9631390

Van der Waal, B. C. W., & Skelton, P. H. (1984). Check listo f fishes of Caprivi. *Madoqua*, *13*(4), 303–320.

Van Ginneken, M., Decru, E., Verheyen, E., & Snoeks, J. (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. https://doi.org/10.5852/ejt.2017.310

Vreven, E., Musschoot, T., Decru, E., Wamuini, L., Obiero, K., Cerwenka, A., & Schliewen, U. K. (2018). The complex origins of mouth polymorphism in the *Labeobarbus* (Cypriniformes: Cyprinidae) of the Inkisi river basin (lower Congo, DRC, Africa): Insights from an integrative approach. *Zoological Journal of the Linnean Society*, *20*(2), 414–482. https://doi.org/10.1093/zoolinnean/zly049

Yang, L., Sado, T., Vincent, H. M., Pasco-Viel, E., Arunachalam, M., Li, J., Wang, X., Freyhof, J., Saitoh, K., Simons, A. M., Miya, M., He, S., & Mayden, R. L. (2015). Phylogeny and polyploidy: Resolving the classification of cyprinine fishes (Teleostei: Cypriniformes). *Molecular Phylogenetics and Evolution*, *85*, 97–116. https://doi.org/10.1016/j.ympev.2015.01.014

Yi, M., Lu, H., Du, Y., Sun, G., Shi, C., Li, X., Tian, H., & Liu, Y. (2021). The color change and stress response of Atlantic salmon (*Salmo salar* L.) infected with *Aeromonas salmonicida*. *Aquaculture Reports*, *20*, 100664. https://doi.org/10.1016/j.aqrep.2021.100664

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