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Research article

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Revalidation of *Enteromius alberti* and presence of *Enteromius cf. mimus* (Cypriniformes: Cyprinidae) in the Lake Edward system, East Africa

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Abstract. A revision was done on the species of *Enteromius* Cope, 1867 (Cypriniformes: Cyprinidae) from the Lake Edward system with a smooth, flexible third unbranched dorsal fin ray without serrations. Specimens with these characteristics had previously been attributed to *E. perince* and *E. stigmatopygus*. A combination of a genetic (COI, mtDNA) and a morphometric approach was used. Based on the COI gene, we found two groups with a distance of 8.5%, though neither of the two corresponded to *E. perince* or *E. stigmatopygus*. One group revealed to be conspecific with *E. alberti*, previously a synonym of *E. stigmatopygus*, described from the Rutshuru River, May-Ya-Moto (DRC, Lake Edward system), and revalidated here. In addition, *E. cercops*, described from the Nzoia River (Kenya, Lake Victoria basin), is put in synonymy with *E. alberti*. The second group was most similar to *E. mimus*, but differed morphologically somewhat from the types of *E. mimus*. Therefore, specimens of this group were identified as *E. cf. mimus*. Morphologically, *E. alberti* can be separated from *E. cf. mimus* based on a higher number of lateral line scales and smaller values for interorbital width, pre-pelvic distance, body depth, maximum and minimum caudal peduncle depth, head width and head depth.

Keywords. *Enteromius cercops*, *Enteromius perince*, *Enteromius stigmatopygus*, integrative taxonomy, synonymy.

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Introduction

With an estimated 367 genera and 3006 species, Cyprinidae is the largest family of freshwater fishes in the world (Nelson *et al.* 2016). One of these genera, *Enteromius* Cope, 1867, occurs only on the African continent and contains about 211 valid species, making it the second largest fish genus in Africa, and the third largest in the world, only exceeded by *Schistura* McClelland, 1838 (228 valid species), and *Haplochromis* Hilgendorf, 1888 (229 valid species) (Froese & Pauly 2019). The genus *Enteromius*, formerly referred to as ‘*Barbus*’ (Berrebi *et al.* 1996), represents a non-monophyletic group that includes most small-sized African diploid barbs (Yang *et al.* 2015; Hayes & Armbruster 2017).

Taxonomic problems in the genus *Enteromius*

There is a general opinion among ichthyologists that cyprinids are a taxonomically difficult group and that many species ‘look the same’, having a rather uniform body shape (Lowe-McConnell 1975; Howes 1991). This specifically holds for *Enteromius*. Specimens of this genus can be attributed to three groups based on the morphology of the third unbranched dorsal fin ray: bony with serrations, bony without serrations, or slender and flexible without serrations (Skelton *et al.* 1991). While these characters seem to be indicative of a common descent on a small geographic scale, as demonstrated in studies on the species from the basins of the Congo River (Van Ginneken *et al.* 2017) and of Lake Edward (Decru *et al.* 2019), on a larger geographic scale, they do not seem to give a reliable phylogenetic signal (Yang *et al.* 2015; Ren & Mayden 2016; Hayes & Armbruster 2017), and point at convergent evolution at higher levels of hierarchy in the trees. Furthermore, the identification of species of *Enteromius* is challenging because of morphological similarities, a limited representation in the literature and because of a lack of identification keys and large-scaled revisions (Van Ginneken *et al.* 2017; Decru *et al.* 2019). Consequently, many specimens in museum collections, as well as the voucher specimens of several sequences on GenBank are misidentified (Hayes & Armbruster 2017). In addition to the paucity of taxonomic data, recent studies on species of *Enteromius* from various regions revealed the presence of many undescribed species (Schmidt *et al.* 2017; Van Ginneken *et al.* 2017). This also implies that the species diversity in *Enteromius* might be of an even much larger magnitude than currently thought. Indeed, if these findings of hidden diversity can be extrapolated to other regions, then an enormous increase of species numbers among the small African barbs is to be expected, which could render *Enteromius* the by far most species-rich, although currently non-monophyletic, fish genus in the world.

It is intriguing to find these small, inconspicuous fish to be so hyperdiverse. However, the mechanisms driving speciation in *Enteromius* have never been investigated. The study of Van Ginneken *et al.* (2017) on some groups of *Enteromius* from the Congo basin, suggested a mainly allopatric mode of speciation, as most lineages are confined to a certain river stretch. Allopatric speciation is probably the mode of speciation by which the majority of riverine fishes arose (Seehausen & Wagner 2014). Still, in the case of *Enteromius*, it is difficult to envisage how allopatric speciation alone can explain some cases of morphological highly similar species occurring in sympatry, as was found in the study of Van Ginneken *et al.* (2017). Furthermore, hybridisation events can also be important in the evolutionary history of *Enteromius*. This has already been documented for several cichlid and cyprinid lineages in Africa (Schwarzer *et al.* 2012; Wagner *et al.* 2012; Levin *et al.* 2017) and specifically for *Enteromius*, Schmidt *et al.* (2017) found cases of introgression in some Kenyan species.

Species of *Enteromius* from the Lake Edward system

The Lake Edward system is situated on the border between the Democratic Republic of the Congo (DRC) and Uganda. The system includes Lake Edward (surface area: 2325 km²), which is one of the smaller East African Great Lakes, Lake George (surface area: 250 km²), the Kazinga Channel, which connects both lakes, and several inflowing rivers and isolated crater lakes. The system is situated in High Africa (*sensu* Roberts 1975), the southern and eastern part of the African continent that lies almost completely above 300 meters. The rivers in High Africa are characterized by having a poor fish fauna that is dominated by Cyprinidae (Roberts 1975; Skelton 1994). This especially holds for the rivers of the Lake Edward system, where *Enteromius* is mainly found (Decru *et al.* 2019). However, not much information is available on the physiochemical characteristics of these rivers (Mbalassa *et al.* 2014). The system is situated at the limit of three ichthyofaunal provinces as described by Roberts (1975): the Nilo-Sudan, the Congo and the East-Coast Provinces. Initially, the system was assigned to the Nilo-Sudan Province (Roberts 1975). However, in a recent study on the fish fauna of the Lake Edward system, it was shown that the Lake Edward system has more affinity with the East-Coast ichthyofaunal Province (Decru *et al.* 2019), confirming the previous assignment of the basin to this province (Snoeks *et al.* 2011).

In the most recent checklist of the ichthyofauna of the Lake Edward system (Decru *et al.* 2019), five species of *Enteromius* were listed: *E. apleurogramma* (Boulenger, 1911), *E. kerstenii* (Peters, 1868), *E. pellegrini* (Poll, 1939), *E. perince* (Rüppell, 1835) and *E. stigmatopygus* (Boulenger, 1903). In that study, the need of a revision of these species was already underscored. *Enteromius apleurogramma*, *E. kerstenii* and *E. pellegrini* all have a bony and serrated third unbranched dorsal fin ray. These species were described from localities in the East Coast Province outside the Lake Edward system. *Enteromius perince* and *E. stigmatopygus*, both with a smooth third unbranched dorsal fin ray, were described from the Nile in Egypt and the White Nile in Sudan, respectively. This renders *E. perince* and *E. stigmatopygus*, together with *Labeo forskalii* Rüppell, 1835, the only fish species from the Lake Edward system that are not shared with other systems of the East Coast Province, but only with the Nile system within the Nilo-Sudan Province (Decru *et al.* 2019). In contrast, the remaining species of *Enteromius*, as well as most other small-sized riverine fishes, are shared with other systems within the East Coast Province and are absent from the Nile. This disparity probably implies an underlying taxonomic problem.

In his review of the Nilotic small barbids, Banister (1987) listed both *E. perince* and *E. stigmatopygus*, but noted that they were difficult to distinguish from each other. Boulenger (1903) reported in the original description of *E. stigmatopygus* that only the anterior scales of the lateral line are pored. Banister (1987), however, mentioned that the number of pored scales along the lateral line is not a good characteristic to distinguish *E. stigmatopygus* from other species. The specimens of the type series of *E. stigmatopygus* are small and he found that the pores start to develop when specimens become larger. The same applies to the development of the barbels. Boulenger (1903) mentioned the absence of barbels in *E. stigmatopygus*. However, Banister (1987) found posterior barbels in the larger type specimens. In addition, he stated that the classification of *Enteromius* relies too much on the number of barbels. In the same study, Banister (1987) mentioned some other characters to distinguish *E. stigmatopygus* from other species. He found *E. stigmatopygus* to be more ‘spotted’ than *E. perince*, and adult specimens to differ from spotted specimens of *E. perince* in the more anterior position of the middle spot. Additionally, according to the description by Banister (1987), *E. perince* has seven well-developed gill rakers on the first ceratobranchial, while *E. stigmatopygus* has only two that are situated on the dorsal part of the first ceratobranchial and papillate tissue (see Banister 1987: 123, fig. 12) on the ventral part. In the same publication, when redescribing *E. stigmatopygus*, he mentioned two to four large gill rakers on the dorsal part and papillate tissue with zero to three low ridges of unknown homology on the ventral part of the first ceratobranchial. Banister (1987) also put *E. alberti* (Poll, 1939), described from the Rutshuru River, May-Ya-Moto (DRC), situated in the southern part of the Lake Edward system, in synonymy with *E. stigmatopygus*. He did this without examining the type specimens of *E. alberti*.

During four recent expeditions to the Lake Edward system (2016–2019, Decru *et al.* 2019), several specimens resembling *E. stigmatopygus* and *E. perince* were collected. It was, however, not possible to assign the specimens to either of these two species, based on the diagnostic characters proposed by Banister (1987). In our study, the *E. stigmatopygus/perince*-like specimens were examined using an integrative approach in order to evaluate their taxonomic status, and to assign them to the correct species.

Material and methods

During the HIPE project (Human impacts on ecosystem health and resources of Lake Edward), four field expeditions to the Ugandan side of the Lake Edward system took place, three during the wet (October 2016, March 2017, March 2019) and one during the dry (January 2018) season. The Congolese side of the system was not sampled due to security issues. Specimens of *Enteromius* were caught using gillnets with different mesh sizes, scoop nets and a backpack electrofisher. After euthanasia with clove oil, for some specimens, a tissue sample (fin clip) was taken for molecular analyses and stored in 100% ethanol. Specimens were then fixed in formalin. At the RMCA (Royal Museum for Central Africa), specimens were rinsed and transferred to 70% EtOH. For morphological analyses, specimens of the first three expeditions were used and specimens of all four expeditions were used for genetic analyses.

In total, we examined 214 specimens, 72 of which both genetically and morphometrically, 70 specimens only genetically and 72 specimens only morphologically ([Supplementary File SM.01](#)). The latter group included the type specimens of *E. perince*, *E. stigmatopygus* and of *E. alberti*, as well as four specimens from a marshy area near Tshambi, identified as *E. alberti*, and mentioned in the original description of *E. alberti*. One of these specimens was too small to take correct measurements of and consequently was excluded from the analyses. The syntypes of *E. mimus* (Boulenger, 1912) and the holotype and seven paratypes of *E. cercops* (Whitehead, 1960) were also examined morphometrically. These species, which stem from other parts of the East Coast and the Nile system (i.e., the regions that border to the Lake Edward system), are most similar to the specimens of *E. stigmatopygus/perince* from Lake Edward, and were therefore included in the morphometric study. From the ten syntypes of *E. mimus*, one was not conspecific with the others because it had serrations on the third unbranched dorsal fin ray and it was the only specimen without a clear melanin pattern. Hence it was not included in our analyses. A lectotype was assigned for *E. alberti* and *E. mimus* in this study.

DNA extraction, PCR amplification and sequencing, DNA analyses

DNA was extracted from finclips using a ‘NucleoSpin® Tissue Kit’ using the standard protocol for human or animal tissue and cultured cells (Macherey-Nagel, Germany). The mitochondrial cytochrome c oxidase I (COI) gene was isolated and amplified using the M13-tailed primer cocktail of Ivanova *et al.* (2007) and the protocol of Decru *et al.* (2016), but using 2.0 instead of 1.0 µl extracted DNA. Amplified PCR products were visualised on 1.2% agarose gels and afterwards purified using ExoSAP (Fermentas). The sequences were determined in two directions, forward and reverse, by Sanger sequencing, executed by the external company Macrogen. The DNA sequences were assembled and visually checked in CodonCode Aligner 4.2.7 (CodonCode Corporation). The consensus sequences were aligned in MEGA 7.0.26 (Kumar *et al.* 2016) and the primer sequences were deleted. A TCS haplotype network (Templeton *et al.* 1992) was generated using PopART (Leigh & Bryant 2015) to visualise the haplotype pattern and to examine geographic structuring. Clusters were identified in the TCS-network, based on genetic differences between the haplotypes.

We searched for COI sequences on GenBank (Clark *et al.* 2016) of specimens, identified as one of the species examined in this study, in order to compare them with our COI sequences from the Lake Edward system ([Supplementary File SM.01](#)). Only five sequences of *E. perince* (LC487172.1 – LC487176.1) from El-Kanater station, northern part of the Nile River, Egypt (Dr Fawzia Salah Ali pers. com.) were

available ([Supplementary File SM.01](#)) (voucher specimens are stored in the National Institute For Oceanography & Fisheries (NIOF), Alexandria, Egypt). The genetic divergence between our sequences and those from GenBank has been assessed.

Morphometric analyses

Twenty-four morphometric measurements were taken with a dial caliper and 13 meristics were counted on each specimen. Most measurements and all counts were done under a binocular microscope (Wild Heerbrugg M3). Measurements were based on Bamba *et al.* (2011) with some modifications. Post-dorsal distance I, post-anal distance I and body depth I were not measured, because of the strong correlation with other measurements. The following measurements were added: head width (width of the head at the level of the posterior margin of the pre-operculum), head depth (depth of the head at the level of the posterior occipital margin), anal fin base length (distance between the articulation base of the first and last anal fin rays), anal fin length (distance from the articulation of the first anal fin ray to the tip of the longest anal fin ray), pectoral fin length (distance from the articulation of the first pectoral fin ray to the tip of the longest pectoral fin ray) and pelvic fin length (distance from the articulation of the first pelvic fin ray to the tip of the longest pelvic fin ray). For all meristics, Bamba (2012) was followed.

The multivariate dataset was explored by Principal Component Analyses (PCA) to reduce the large number of variables into a few meaningful axes that are linear combinations of the original variables (Manly 1994; Snoeks 2004; Decru *et al.* 2012). Measurements and meristics were analysed separately. Log-transformed data were used for the PCA on the measurements and analysed with a covariance matrix. The first axis of the PCA on log-transformed measurements can be interpreted as a proxy for size (Bookstein *et al.* 1985). Hence, subsequent axes can be plotted against the first axis to verify possible size effects. The raw data were used for the PCA on the meristics based on the correlation matrix. Invariable meristics were excluded from the PCAs. Data for the barbels were not included in the analyses, as the barbels were small and difficult to measure and hence their measurements were prone to errors.

A first PCA was performed on the 72 specimens from the Lake Edward system that were analysed genetically to evaluate the morphological differences among specimens from different genetic clades. To find possible significant differences between these groups, univariate comparisons were performed with non-parametric Mann-Whitney U-tests (MWU), with sequential Bonferroni corrections (Rice 1989). For measurements, these comparisons were restricted to subsets of specimens that belong to a similar size class (46.4–53.8 mm SL; with $p = 0.6888$ for SL). This was done to avoid allometric interference. Scatterplots of individual measurements (% SL) were made to visualize between-group differences taken into account possible size-effects. Based on this first set of analyses, additional specimens for which no genetic data were available, were measured and assigned to one of the groups in order to enlarge the size ranges of these groups. This also allowed for comparison with the type series of similar species. Hence, in a second series of analyses, PCAs were performed to compare each group separately with all of the studied type specimens of *E. perince*, *E. stigmatopygus*, *E. alberti*, *E. mimus* and *E. cercops*, and with the specimens from Tshambi identified as *E. alberti*.

The statistical analyses were executed in R Studio 1.1.453 (RStudio Team 2016) with R ver. 3.5.1 (R Core Team 2018). Scatterplots and PCAs were made using the package ‘vegan’ ver. 2.5-2 (Oksanen *et al.* 2018) and the package ‘factoextra’ ver. 1.0.5 (Kassambara & Mundt 2017).

Results

We successfully obtained 137 COI sequences (trimmed to 651 bp) ([Supplementary File SM.01](#)). The haplotype network of the specimens from the Lake Edward system (Fig. 1) showed two clear groups with a genetic divergence of 8.5%. No geographical structuring was observed. We refer to these groups as group A, the smallest group ($n = 36$), and group B, the largest group ($n = 101$). The sequences of

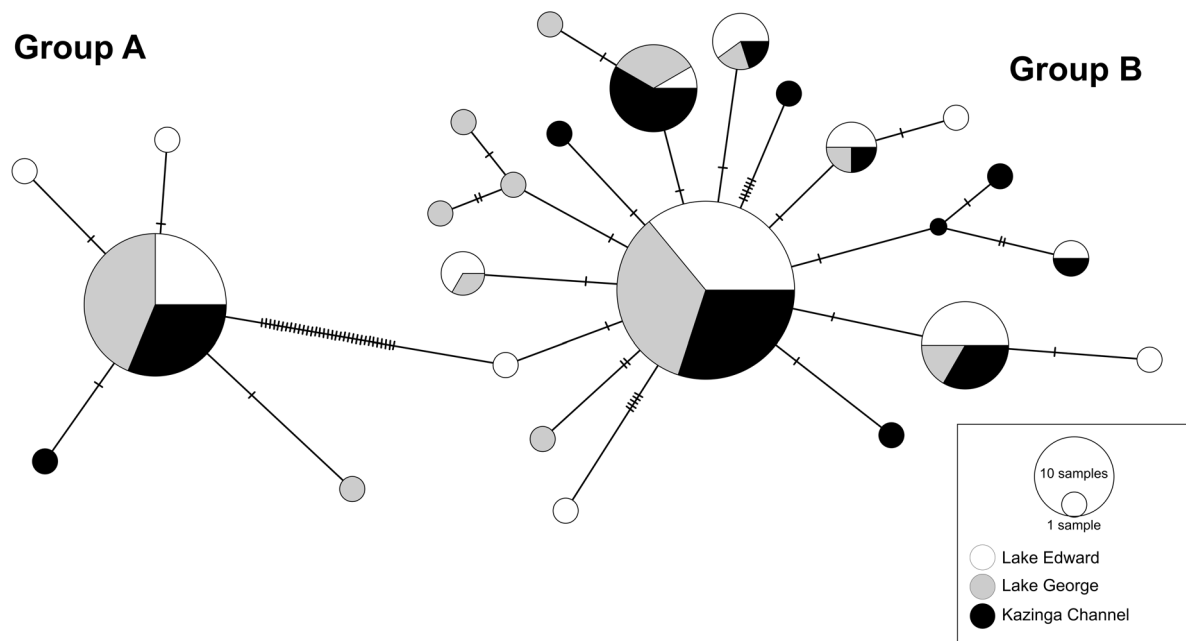


Fig. 1. Haplotype network of 651-bp-long COI sequences ($n = 137$) of the specimens of *Enteromius* Cope, 1867 with a smooth, flexible last unbranched dorsal fin ray from the Lake Edward system. Each circle represents a haplotype, with the size of the circles indicating the number of individuals with this haplotype and the colour indicating the different parts of the basin. Each bar represents a mutation between two haplotypes.

E. perince from Egypt, obtained from GenBank, had a genetic difference of 12% from the sequences of our groups A and B, and were therefore not integrated in the haplotype network.

Morphometric analyses

Of the 137 specimens that were analysed genetically, 71 specimens were also analysed morphometrically. A first PCA on the log-transformed measurements of these specimens resulted in a separation on PC2 (Fig. 2) of the two groups that were delineated based on the genetic data. PC1 represented an inverted proxy of size, with larger specimens having lower values on PC1 than smaller specimens. The most important loadings for PC2 were for the post-anal distance and the maximum and minimum caudal peduncle depth (Supplementary File SM.02). In the PCA on meristics, the two groups partially overlapped (not illustrated).

Based on Mann-Whitney U (MWU) tests with sequential Bonferroni correction, 13 measurements and three meristics were significantly different between the two groups, of which the three meristics were highly significant (Table 1). Individual scatterplots were made for the most significant measurements (% SL) (Fig. 3): interorbital width, pre-pelvic distance, body depth, maximum caudal peduncle depth, minimum caudal peduncle depth, head width, and head depth. For all of these measurements, the ranges per se overlapped because of allometry, but for specimens of similar size classes, the two groups could be distinguished from each other, with specimens of group B having higher values for all these measurements. Based on the results of the first series of analyses discussed above, we were able to identify 16 additional specimens as members of group A, and 22 additional specimens as members of group B. These specimens were added to the dataset to enlarge the size ranges of the two groups, allowing for a better comparison of the groups with the type series of the relevant species. Subsequently, each

Table 1. Results of the MWU tests with Bonferroni correction on measurements (% SL) of specimens of similar size classes (46.4–53.8 mm), and on meristics of all specimens, on the two groups of *Enteromius* Cope, 1867. Significant values ($\alpha = 0.05$) are in bold; highly significant values ($\alpha = 0.001$) are in bold and underlined.

| Measurements (% SL) | Group A (n = 8) × Group B (n = 10) |
|---|--|
| Head length (HL) | 0.0831 |
| Eye diameter (ED) | 0.0029 |
| Snout length (SnL) | 0.0062 |
| Pre-operculum distance (PrOpD) | 0.0155 |
| Interorbital width (IOW) | < 0.0001 |
| Pre-dorsal distance (PrDD) | 0.0044 |
| Post-dorsal distance (PoDD) | 0.0002 |
| Dorsal fin base length (DoFBL) | 0.5726 |
| Dorsal fin length (DoFL) | 0.3599 |
| Pre-pectoral distance (PrPecD) | 1.0000 |
| Pre-pelvic distance (PrPelD) | < 0.0001 |
| Pre-anal distance (PrAD) | 0.0014 |
| Post-anal distance (PoAD) | 0.0009 |
| Body depth (BD) | < 0.0001 |
| Maximum caudal peduncle depth (MxCPD) | < 0.0001 |
| Minimum caudal peduncle depth (MnCPD) | < 0.0001 |
| Pre-occipital distance (PreOcD) | 0.0343 |
| Head width (HW) | < 0.0001 |
| Anal fin base length (AnFBL) | 0.0205 |
| Anal fin length (AFL) | 0.0009 |
| Pectoral fin length (PcFL) | 0.5726 |
| Pelvic fin length (PlvFL) | 0.4082 |
| Head depth (HD) | < 0.0001 |
| Meristics | Group A (n = 22) × Group B (n = 50) |
| Lateral line scales (LLS) | < 0.0001 |
| Total number of lateral line scales (LLS total) | < 0.0001 |
| Pre-dorsal scales (PDSc) | 0.0266 |
| Scales lateral line – pelvic fin (LPSc) | 0.1268 |
| Scales lateral line – belly (L-BSc) | 0.2653 |
| Branched dorsal fin rays (DFR branched) | 0.1303 |
| Branched anal fin rays (AFR branched) | 0.1450 |
| Branched pectoral fin rays (PecFR branched) | < 0.0001 |
| Unbranched pelvic fin rays (PelFR unbranched) | 0.4942 |
| Branched pelvic fin rays (PelFR branched) | 0.6916 |
| Gill rakers upper limb first gill arch (GrUp) | 0.6935 |
| Gill rakers lower limb first gill arch (GrLow) | 0.8736 |
| Total gill rakers (GrTot) | 0.7320 |

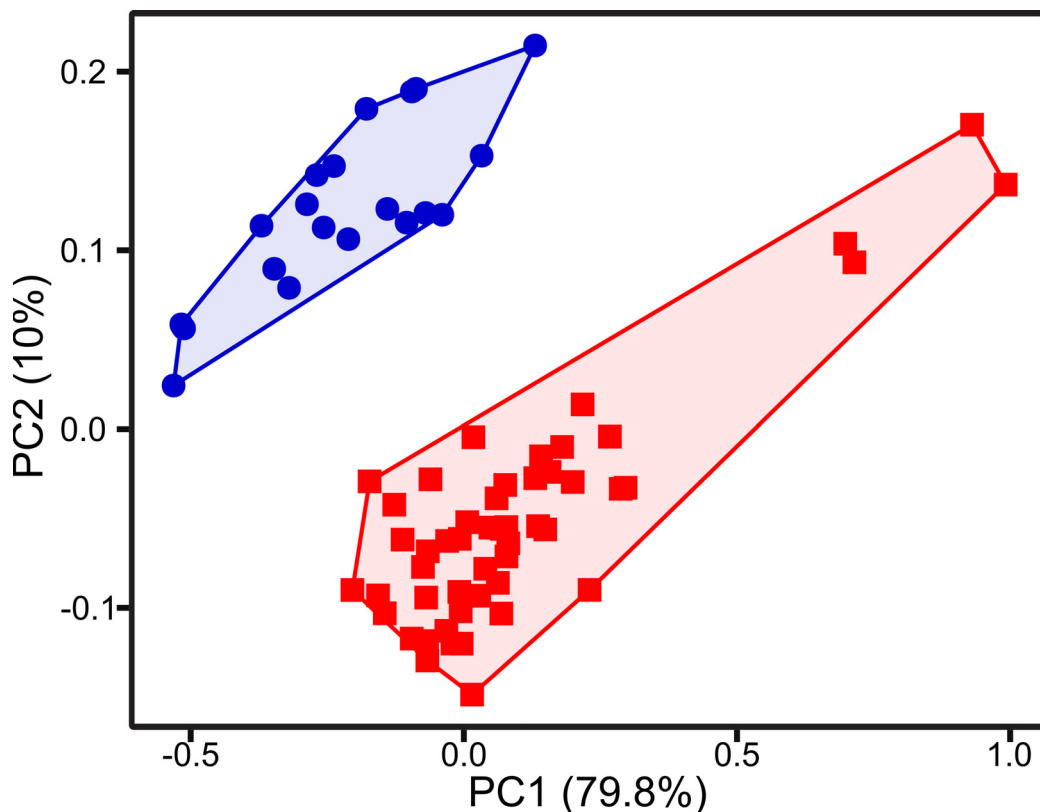


Fig. 2. Scatterplot of PC2 against PC1 of a PCA on 24 log-transformed measurements on 71 specimens of *Enteromius* Cope, 1867. Specimens of the genetic groups A (●) (n = 21) and B (■) (n = 50) are indicated separately.

group was compared with the types of *E. alberti*, *E. cercops*, *E. mimus*, *E. perince* and *E. stigmatopygus* and the additional specimens from Tshambi identified as *E. alberti*.

A PCA on log-transformed measurements was performed on the specimens assigned to group A, all the type specimens included in this study and the specimens from Tshambi (Fig. 4a). On a scatterplot of PC2 vs PC1, specimens belonging to group A were separated from *E. perince*, *E. stigmatopygus* and the specimens from Tshambi. They were also separated from the types of *E. mimus*, except for one specimen. The holotype and paratypes of *E. cercops* and two of the three types of *E. alberti* fell, however, into the polygon of group A. The most important loadings for PC2 were the maximum caudal peduncle depth, the interorbital width and the body depth (Supplementary File SM.03).

In a scatterplot of the two main PCs of a PCA on the meristics, the type specimens of *E. alberti* fell within group A and *E. cercops* overlapped with group A (Fig. 4b). Here, group A also partially overlapped with *E. perince*, due to one specimen, but it was completely separated from the specimens from Tshambi, *E. mimus* and *E. stigmatopygus* on PC1. The most important loadings for PC1 were the number of scales on the lateral line, the number of branched pectoral fin rays and the number of scales between the origin of the dorsal fin and the lateral line (Supplementary File SM.04). As the specimens from Tshambi, identified as *E. alberti*, fell separately from the types of *E. alberti*, these were most probably misidentified. To explore possible differences between group A, *E. alberti* and *E. cercops*, subsequent PCAs were performed restricted to these three groups. In these analyses, still no separation of the three groups was obtained (not illustrated).

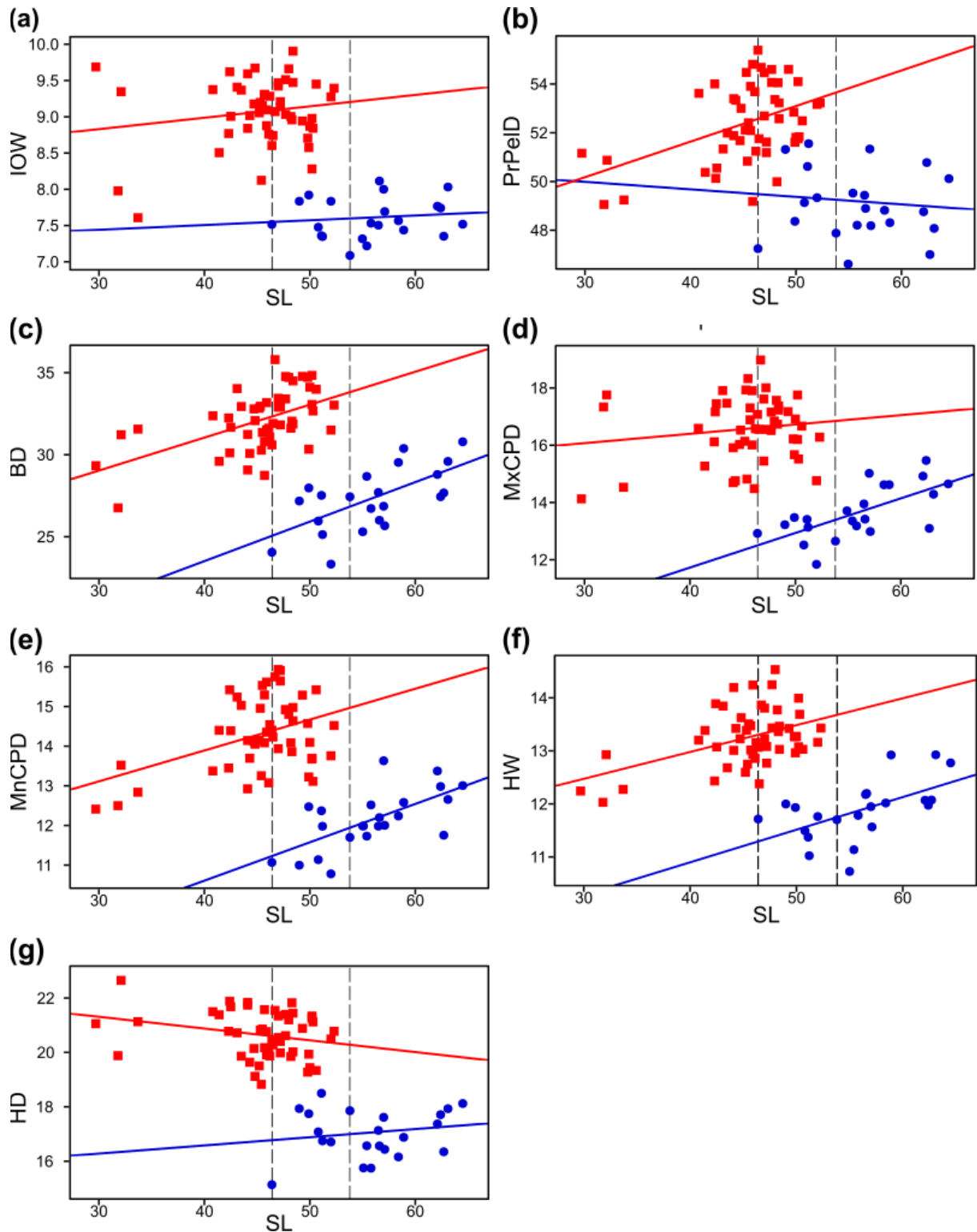


Fig. 3. Scatterplots of (a) interorbital width (IOW), (b) pre-pelvic distance (PrPeID), (c) body depth (BD), (d) maximum caudal peduncle depth (MxCPD), (e) minimum caudal peduncle depth (MnCPD), (f) head width (HW), and (g) head depth (HD) in % SL against SL (in mm) on 72 specimens of *Enteromius* Cope, 1867. The genetic groups A (●) (n = 22) and B (■) (n = 50) are indicated separately. The dashed lines indicate the size class used for the MWU tests.

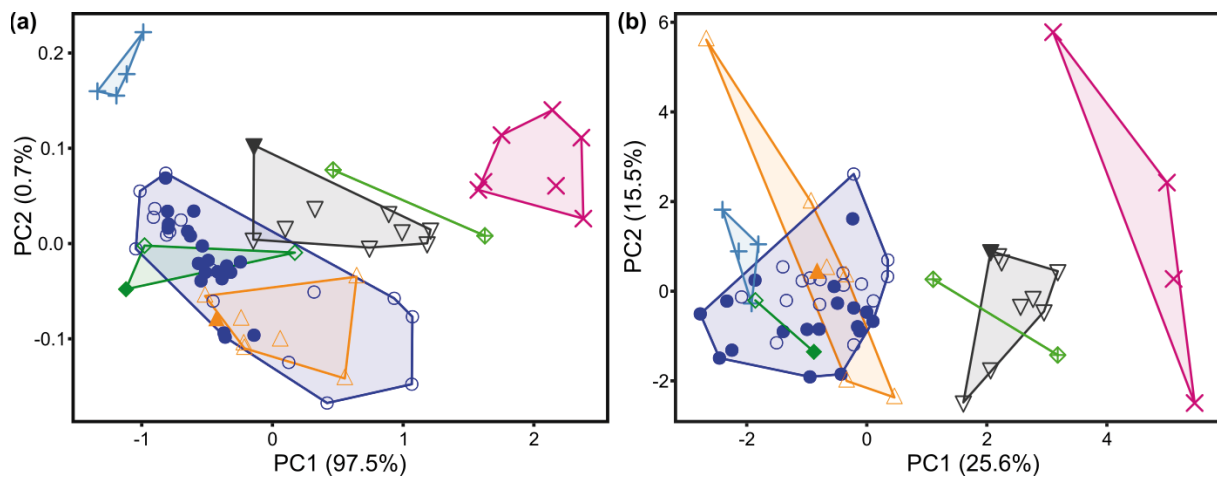


Fig. 4. Scatterplots of PC2 against PC1 of the PCA on **(a)** 24 log-transformed measurements ($n = 69$) and **(b)** on 15 meristics ($n = 62$). Specimens of group A, the filled circles (●) represent the genetically analysed specimens, the open circles (○) indicate the additional specimens. Specimens of *E. alberti* (Poll, 1939) (lectotype) (◆), *E. alberti* (paralectotypes) (◇), specimens from Tshambi (⊕), *E. cercops* (Whitehead, 1960) (holotype) (▲), *E. cercops* (paratypes) (△), *E. mimus* (Boulenger, 1912) (lectotype) (▼), *E. mimus* (paralectotypes) (▽), *E. perince* (Rüppell, 1835) (syntypes) (+) and *E. stigmatopygus* (Boulenger, 1903) (syntypes) (×).

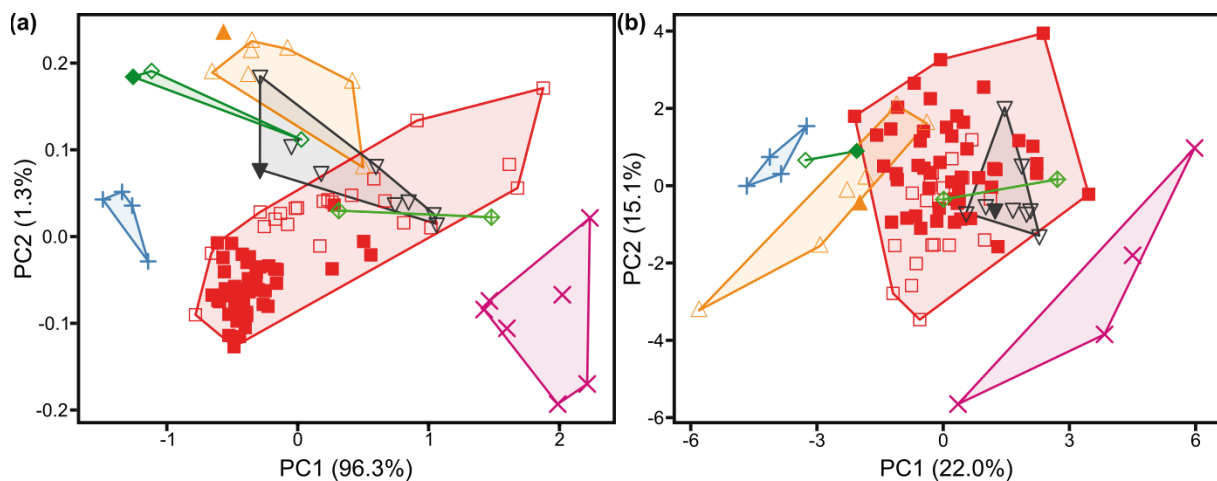


Fig. 5. Scatterplots of PC2 against PC1 of **(a)** the PCA ($n = 105$) on 24 log-transformed measurements and **(b)** the PCA ($n = 95$) on 15 meristics. Specimens of group B, the filled squares (■) represent the genetic analysed specimens, the open squares (□) indicate the additional specimens. Specimens of *E. alberti* (Poll, 1939) (lectotype) (◆), *E. alberti* (paralectotypes) (◇), specimens from Tshambi (⊕), *E. cercops* (Whitehead, 1960) (holotype) (▲), *E. cercops* (paratypes) (△), *E. mimus* (Boulenger, 1912) (lectotype) (▼), *E. mimus* (paralectotypes) (▽), *E. perince* (Rüppell, 1835) (syntypes) (+) and *E. stigmatopygus* (Boulenger, 1903) (syntypes) (×).

Specimens belonging to group B were also compared with the type specimens of the selected species and the specimens from Tshambi. In the PCA on the log-transformed measurements, group B was separated from most of the type specimens, but partially overlapped with those of *E. mimus* and with one paratype of *E. cercops* on PC2 for specimens with similar sizes (Fig. 5a). Furthermore, one of the specimens from Tshambi was situated within the polygon of group B, while the other one was located just outside of the polygon. The most important loadings for PC2 were the anal fin base length, the interorbital width and the anal fin length (Supplementary File SM.05).

Another PCA was performed on the meristics of group B and the selected type specimens. Here, both specimens from Tshambi fell within group B. Almost all types of *E. mimus* were situated within the polygon of group B, except for one, which was located just outside of the polygon. Group B partially overlapped with *E. cercops* (Fig. 5b). The most important loadings for PC1 were the number of scales on the lateral line, around the caudal peduncle and below the lateral line and, for PC2, the total number of gill rakers, the number of gill rakers on the lower part of the first gill arch and the number of pre-dorsal scales (Supplementary File SM.06).

These PCAs (Fig. 5) illustrated that the specimens from Tshambi, identified as *E. alberti*, were most probably conspecific to our group B. This latter group seemed to be most similar to *E. mimus*. Therefore, additional PCAs on meristics and log-transformed measurements were performed including only group B, with the inclusion of the specimens from Tshambi, and the types of *E. mimus*. For the meristics, the syntypes of *E. mimus* fell completely within the range of group B for the first two axes (not illustrated). For the log-transformed measurements, however, only a partial overlap was observed on PC2 (Fig. 6).

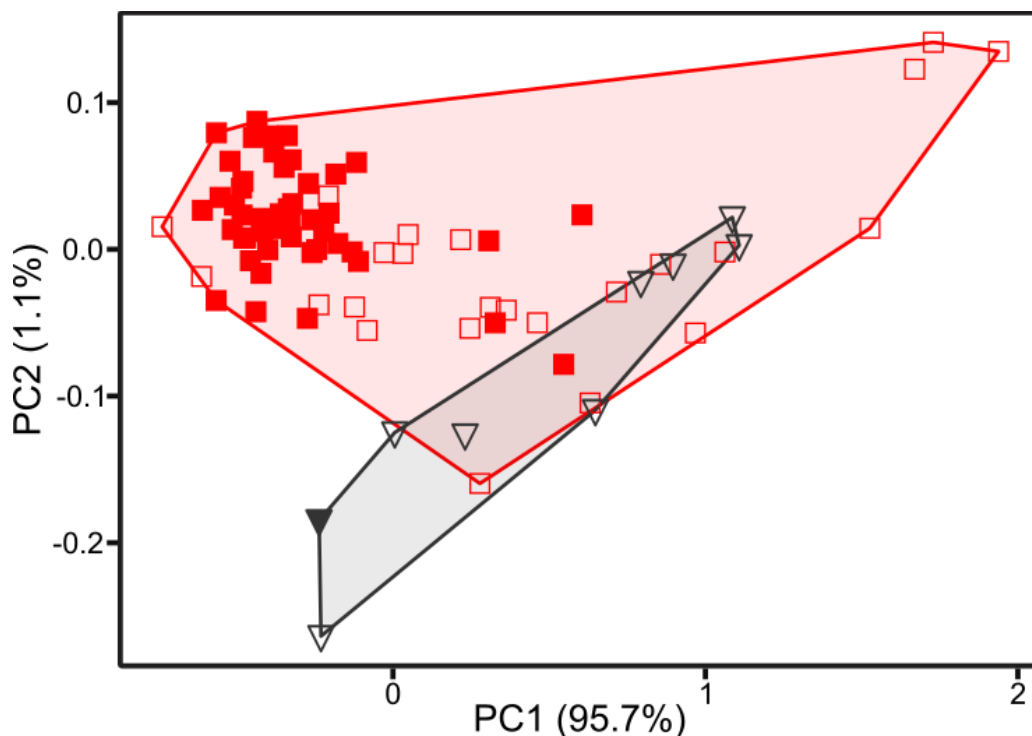


Fig. 6. Scatterplot of PC2 against PC1 of the PCA (n = 83) on 24 log-transformed measurements. For group B, the filled squares (■) represent the specimens used for the genetic analysis, the open squares (□) indicate the additional specimens of the Lake Edward system and the two specimens from Tshambi. Specimens of *E. mimus* (Boulenger, 1912) (lectotype) (▼) and *E. mimus* (paralectotypes) (▽).

Here, the most important loadings for PC2 were for the snout length, the pelvic fin length and the interorbital width ([Supplementary File SM.07](#)).

In the analysis of measurements restricted to group B, one of the types of *E. alberti* was situated within the polygon of the types of *E. mimus* (Fig. 5a). In that of the measurements of group A (Fig. 4a), the same specimen was situated closest to the polygon of the types of *E. mimus*. This specimen had an aberrant value for the number of lateral line scales (23) compared to the other types of *E. alberti* (31 and 32), which corresponds more to the number of lateral line scales found in group B (21 to 31 with median 26). Furthermore, the aberrant specimen had 32 vertebrae in total, while the other two types of *E. alberti* had 35 vertebrae. The total number of vertebrae was 34 to 35 for specimens in group A (n = 4) and 31 to 33 in group B (n = 4). Based on these results, the aberrant type specimen of *E. alberti* could be assigned to group B.

Nomenclature and synonyms

Class Actinopterygii Klein, 1885
Subclass Neopterygii Regan, 1923
Division Teleostei Müller, 1846
Order Cypriniformes Rafinesque, 1810
Family Cyprinidae Rafinesque, 1815

Genus *Enteromius* Cope, 1867

The results confirmed the occurrence of two syntopic species of *Enteromius* with a smooth dorsal fin ray in the Lake Edward system. Specimens of group A were conspecific with the types of *E. alberti*, except for one type specimen, which was assigned to group B, and with the holotype and paratypes of *E. cercops*. *Enteromius alberti* used to be considered a synonym of *E. stigmatopygus*. Based on our results, and following the principle of priority for species names, we propose to revalidate *E. alberti* with *E. cercops* as its junior synonym. A redescription of *E. alberti* is provided based on the lectotype (here designated) (Fig. 7a) and one paralectotype of *E. alberti*, the type series of *E. cercops*, here synonymised with *E. alberti*, and the additional specimens from the Lake Edward system examined in this study and identified as *E. alberti* (n = 37). The other paralectotype of *E. alberti*, which was revealed not to be conspecific with *E. alberti*, was not included in the redescription. The measurements and meristics can be found in Table 2. An illustration of a fresh specimen of *E. alberti*, captured during the HIPE expeditions is provided in Fig. 7b.

The specimens of group B were most similar to *E. mimus*, though the PCA on log-transformed measurements (Fig. 6) suggested some differences. Therefore, we decided to assign the specimens of group B to *E. cf. mimus* with “cf” indicating specimens that are comparable to *E. mimus* but whose identification is uncertain (Decru *et al.* 2016). Because of the unsuitable original description of *E. mimus* for modern taxonomic purposes, we decided to make a redescription based on the lectotype (here designated) (Fig. 8) and eight of the nine paralectotypes of *E. mimus*. We found one paralectotype to have a serrated dorsal fin ray; therefore, it was considered not to be conspecific with the other types and excluded from the redescription. Specimens from the Lake Edward system identified as *E. cf. mimus*, the specimens from Tshambi and the aberrant lectotype of *E. alberti* were not included in the redescription, but their measurements and meristics are given in Table 2. A picture of a fresh specimen of *E. cf. mimus* is given in Fig. 9.

For both redescribed species, a lectotype was chosen from the syntypes. For *E. alberti*, this is the specimen illustrated in the original description by Poll (1939), which is also the largest specimen. The lectotype of *E. mimus* is the specimen that resembles most the original figure of *E. mimus* in the *Catalogue of the Fresh-water Fishes of Africa in the British Museum (Natural History)*, Volume IV, by Boulenger (1916).

Table 2 (continued on the next page). Measurements and meristics of *Enteromius alberti* (Poll, 1939) (n = 47, * = 46, ** = 45), the types of *Enteromius mimus* (Boulenger, 1912) (n = 9), and *Enteromius cf. mimus* (n = 76, * = 75, ** = 74, *** = 73).

| | <i>E. alberti</i> | | | | <i>E. mimus</i> | | | | <i>E. cf. mimus</i> | | | |
|-------------------------------|-------------------|-----------|-------|------|-----------------|-----------|------|------|---------------------|-------|------|--|
| | Lectotype | Min.-Max. | Mean | S.D. | Lectotype | Min.-Max. | Mean | S.D. | Min.-Max. | Mean | S.D. | |
| Standard length (mm) | 74.3 | 26.5-74.3 | 53.4 | 12.1 | 43.6 | 23.2-45.6 | 32.4 | 8.5 | 16.9-55.1 | 41.3 | 9.0 | |
| Measurements (%SL) | | | | | | | | | | | | |
| Head length | 21.6 | 20.5-27.5 | 22.7 | 1.5 | 23.5 | 23.3-27.8 | 25.8 | 1.7 | 22.1-30.3 | 25.1 | 1.8 | |
| Eye diameter | 6.7 | 5.9-9.6 | 7.5 | 0.8 | 7.9 | 7.9-9.6 | 8.7 | 0.5 | 7.4-10.0 | 8.6 | 0.6 | |
| Snout length | 6.9 | 4.2-6.9 | 5.8 | 0.7 | 5.1 | 4.1-7.1 | 6.0 | 1.0 | 4.6-8.3 | 7.0 | 0.7 | |
| Pre-opercular distance | 15.2 | 13.9-19.8 | 16.1 | 1.3 | 16.5 | 15.6-21.8 | 18.2 | 1.8 | 15.7-20.6 | 17.9 | 1.1 | |
| Interorbital width | 7.5 | 5.8-8.3 | 7.3 | 0.6 | 8.1 | 6.3-8.3 | 7.8 | 0.6 | 6.9-9.9 | 8.7 | 0.7 | |
| Pre-dorsal distance | 46.9 | 45.7-51.3 | 49.0 | 1.4 | 50.0 | 48.4-53.2 | 51.1 | 1.5 | 48.9-56.4 | 52.0 | 1.6 | |
| Post-dorsal distance | 41.5 | 33.3-43.3 | 39.1 | 2.1 | 39.6 | 34.8-40.4 | 38.1 | 2.1 | 31.0-39.9 | 35.9 | 2.0 | |
| Dorsal fin base length | 15.3 | 11.0-17.1 | 14.3 | 1.1 | 15.4 | 12.4-15.4 | 14.2 | 1.1 | 11.4-15.6 | 13.7 | 0.9 | |
| Dorsal fin length | 24.1 | 23.7-31.1 | 26.6 | 1.6 | 31.4 | 25.4-31.4 | 28.6 | 1.9 | 23.2-30.7 | 26.9* | 1.5 | |
| Pre-pectoral distance | 23.8 | 22.7-29.7 | 25.1 | 1.7 | 26.0 | 26.0-29.0 | 27.4 | 1.2 | 24.9-32.7 | 28.1 | 1.6 | |
| Pre-pelvic distance | 47.0 | 44.8-53.3 | 49.2 | 1.7 | 53.1 | 49.1-56.0 | 51.4 | 2.5 | 48.4-55.4 | 52.1 | 1.7 | |
| Pre-anal distance | 67.4 | 65.1-73.0 | 69.3 | 1.8 | 74.5 | 68.4-74.8 | 72.4 | 2.2 | 68.8-79.1 | 73.4 | 2.2 | |
| Post-anal distance | 22.5 | 16.3-24.2 | 21.1 | 1.7 | 16.4 | 16.3-19.3 | 17.8 | 1.1 | 14.8-23.9 | 18.0 | 1.8 | |
| Body depth | 26.4 | 21.7-31.2 | 26.9 | 2.3 | 34.3 | 26.5-34.3 | 30.1 | 2.2 | 23.5-35.8 | 31.0 | 2.6 | |
| Maximum caudal peduncle depth | 12.8 | 11.8-15.5 | 13.6 | 1.0 | 16.5 | 12.9-16.5 | 14.6 | 1.1 | 8.7-19.0 | 16.0 | 1.7 | |
| Minimum caudal peduncle depth | 11.6 | 10.0-13.6 | 12.0 | 0.8 | 13.5 | 11.1-14.0 | 12.5 | 1.0 | 7.1-15.9 | 13.7 | 1.5 | |
| Pre-occipital distance | 17.0 | 16.6-21.8 | 18.6 | 1.3 | 19.7 | 18.9-22.4 | 20.8 | 1.1 | 18.7-23.2 | 20.5 | 1.1 | |
| Head width | 12.4 | 10.4-14.2 | 12.0 | 0.7 | 12.2 | 12.2-13.7 | 12.9 | 0.5 | 11.6-14.5 | 13.2 | 0.6 | |
| Anal fin base length | 8.4 | 6.7-9.3 | 8.0 | 0.6 | 8.5 | 7.3-8.7 | 8.0 | 0.6 | 6.2-10.3 | 7.5 | 0.8 | |
| Anal fin length | 18.0 | 16.7-21.9 | 18.9 | 1.2 | 18.7 | 18.0-19.7 | 19.0 | 0.6 | 14.4-21.8 | 17.7 | 1.3 | |
| Pectoral fin length | 18.1 | 16.7-20.4 | 18.6 | 1.0 | 19.7 | 16.6-20.8 | 19.0 | 1.2 | 13.9-21.4 | 18.5 | 1.4 | |
| Pelvic fin length | 18.8 | 15.0-20.9 | 18.0* | 1.3 | 22.4 | 18.2-22.4 | 20.4 | 1.4 | 14.4-21.3 | 18.5 | 1.4 | |
| Head depth | 16.5 | 15.1-19.0 | 17.3 | 0.9 | 21.8 | 17.8-21.8 | 20.2 | 1.2 | 18.8-22.6 | 20.6 | 0.8 | |

Table 2 (continued).

| Meristics | <i>E. alberti</i> | | | <i>E. minus</i> | | | <i>E. cf. minus</i> | | |
|---|-------------------|-----------|--------|-----------------|-----------|--------|---------------------|--------|--|
| | Lectotype | Min.–Max. | Median | Lectotype | Min.–Max. | Median | Min.–Max. | Median | |
| Total number of lateral line scales | 31 | 27–34 | 31 | 24 | 24–27 | 25 | 21–31 | 26 | |
| Scales between dorsal fin and lateral line | 4.5 | 4.5–4.5 | 4.5 | 3.5 | 3.54–4.5 | 3.5 | 3.5–4.5 | 4.5 | |
| Pre-dorsal scales | 10 | 9–13 | 10 | 10 | 9–10 | 9 | 9–12 | 10 | |
| Circumpeduncular scales | 12 | 12–16 | 12 | 12 | 11–12 | 12 | 10–12 | 12*** | |
| Scales between lateral line and pelvic fin | 2 | 2–4 | 3 | 4 | 3–4 | 3 | 2–4 | 3* | |
| Scales between lateral line and belly | 4.5 | 3.5–5.5 | 4.5* | 4.5 | 3.5–4.5 | 3.5 | 3.5–4.5 | 4.5** | |
| Unbranched dorsal-fin rays | 3 | 3–3 | 3 | 3 | 3–3 | 3 | 3–3 | 3* | |
| Branched dorsal-fin rays | 8 | 7–9 | 8 | 8 | 7–8 | 8 | 6–8 | 8* | |
| Unbranched anal-fin rays | 3 | 3–3 | 3 | 3 | 3–3 | 3 | 3–3 | 3 | |
| Branched anal-fin rays | 5 | 5–6 | 5 | 5 | 5–6 | 5 | 4–6 | 5 | |
| Unbranched pectoral-fin rays | 1 | 1–1 | 1 | 1 | 1–1 | 1 | 1–1 | 1 | |
| Branched pectoral-fin rays | 14 | 13–16 | 14* | 14 | 12–14 | 13 | 11–15 | 14 | |
| Unbranched pelvic-fin rays | 1 | 1–2 | 1 | 1 | 1–1 | 1 | 1–2 | 1 | |
| Branched pelvic-fin rays | 7 | 6–8 | 7 | 7 | 7–7 | 7 | 5–8 | 7 | |
| Gill rakers upper part first ceratobranchial | 2 | 0–3 | 1** | 1 | 1–4 | 1 | 0–3 | 1* | |
| Gill rakers lower part first ceratobranchial | 2 | 1–5 | 3** | 3 | 0–4 | 3 | 0–6 | 3* | |
| Total number of gill rakers first ceratobranchial | 5 | 3–8 | 5** | 5 | 3–6 | 5 | 2–9 | 5* | |

The sampling sites of the two species in the Lake Edward system and the type localities of *E. mimus*, *E. alberti* and *E. cercops* are illustrated in Fig. 10. The specimens from Tshambi, initially identified as *E. alberti*, are indicated as *E. cf. mimus* on the map, as found in the present study.

***Enteromius alberti* (Poll, 1939)**

Fig. 7a–b, Table 2

Enteromius cercops (Whitehead, 1960) (here synonymised). syn. nov.

Diagnosis

Enteromius alberti (Fig. 7a–b) belongs to the group of species of *Enteromius* with a flexible last unbranched dorsal fin ray that lacks serrations along its posterior edge. A comparison was made with other species of *Enteromius* from this group from the East Coast and Nilo-Sudan ichthyofaunal provinces (list made based on information available in, e.g., Greenwood 1962; Okaronon *et al.* 1997; Seegers *et al.* 2003; Schmidt *et al.* 2017; Froese & Pauly 2018). *Enteromius alberti* can easily be distinguished from the other species of this group from the East Coast and Nilo-Sudan ichthyofaunal regions by the following combination of characteristics (data from original description, unless otherwise stated): a complete lateral line vs an incomplete lateral line in *E. atkinsoni* (Bailey, 1969), *E. pumilus* (Boulenger, 1901), *E. serengetiensis* (Farm, 2000), *E. tongaensis* (Rendahl, 1935) and *E. toppini* (Boulenger, 1916); two pairs of barbels vs one pair in *E. pseudotoppini* (Seegers, 1996), and no barbels in *E. anema* (Boulenger, 1903) and *E. profundus* (Greenwood, 1970); one to three dark spots on the flanks, which



Fig. 7. (a) Lectotype of *Enteromius alberti* (Poll, 1939) (MRAC 64723) with 74.3 mm SL. **(b)** Fresh specimen of *E. alberti* (RMCA 2018.008.P.0248 HP 3246) with 62.4 mm SL.

sometimes fuse into a mid-lateral line in preserved specimens, starting posterior to the operculum vs a dark line running from the tip of the snout to the caudal fin base in *E. bifrenatus* (Fowler, 1935) and *E. yongei* (Whitehead, 1960), and a thin dark line from the beginning of the operculum to the caudal fin base in *E. viviparus* (Weber, 1897); 12 scales around the caudal peduncle, with one aberrant specimen in the paratypes of *E. cercops* (16), vs 8 in *E. leonensis* (Boulenger, 1915), 9–10 in *E. venustus* (Bailey, 1980), and 10 in *E. magdalenae* (Boulenger, 1906) and *E. yeiensis* (Johnsen, 1926); 4.5 scales between the dorsal fin base and the lateral line vs 3.5 in *E. radiatus* (Peters, 1853) (Greenwood 1970), 5.5 in *E. unitaeniatus* (Günther, 1867), and 6 in *E. usambarae* (Lönnberg, 1907); a dorsal fin length which is larger than the head length vs a dorsal fin length equal to the head length in *E. innocens* (Pfeffer, 1896); a body depth which is larger than the head length vs a body depth which is equal to the head length in *E. nigriensis* (Boulenger, 1903) and *E. trispilopleura* (Boulenger, 1902); a pectoral fin length which is $\frac{5}{6}$ of the head length vs $\frac{3}{4}$ in *E. lineomaculatus* (Boulenger, 1903), and $\frac{2}{3}$ to $\frac{3}{4}$ in *E. neglectus* (Boulenger, 1903) (Boulenger 1907); a maximum caudal peduncle depth which is $\frac{3}{5}$ of the head length vs $\frac{2}{5}$ in *E. quadripunctatus* (Pfeffer, 1896). *Enteromius alberti* differs from *E. perince* by a combination of a smaller body depth [21.7–31.2% SL (mean 26.9) vs 33.8–37.5 (35.0)], a smaller minimum caudal peduncle depth [10.0–13.6% SL (mean 12.0) vs 15.0–16.4 (15.5)], and a smaller maximum caudal peduncle depth [11.8–15.5% SL (mean 13.6) vs 17.7–19.4 (18.8)]. *Enteromius alberti* differs from *E. stigmatopygus* by a combination of a higher number of lateral line scales [27–34 (median 31) vs 20–25 (21)], a smaller pre-dorsal distance [45.7–51.3% SL (mean 49.0) vs 51.9–55.8 (53.8)] and a smaller pre-occipital distance [16.6–21.8% SL (mean 18.6) vs 22.1–27.3 (24.0)]. *Enteromius alberti* differs from *E. mimus* by a higher number of lateral line scales [27–34 (median 31) vs 24–27 (25)], a smaller pre-anal distance [65.1–73.0% SL (average 69.3) vs 68.4–74.8 (72.4)], a larger post-anal distance [16.3–24.2% SL (average 21.1) vs 16.3–19.3 (17.8)], a smaller body depth [21.7–31.2% SL (average 26.9) vs 26.5–34.3 (30.1)], a smaller head depth [15.1–19.0% SL (average 17.3) vs 17.8–21.8 (20.2)] and a smaller pelvic fin length [15.0–20.9% SL (average 18.0) vs 18.2–22.4 (20.4)] (Table 2). Specimens of *E. alberti* differ from the population of *E. cf. mimus* from the Lake Edward system by a smaller head depth. In general, a specimen with a head depth smaller than 19% of the standard length can be assigned to *E. alberti* (only one specimen had a higher value). Specimens with a head depth larger than 19% of the standard length can be assigned to *E. cf. mimus* (only one specimen had a lower value). Other characters to distinguish *E. alberti* from *E. cf. mimus* are the higher number of lateral line scales [27–34 (median 31) vs 21–31 (26)], the smaller interorbital width [5.8–8.3% SL (mean 7.3) vs 6.9–9.9 (8.7)], the smaller pre-pelvic distance [44.8–53.3% SL (mean 49.2) vs 48.4–55.4 (52.1)], the smaller body depth [21.7–31.2% SL (mean 26.9) vs 23.5–35.8 (31.0)], the smaller maximum [11.8–15.5% SL (mean 13.6) vs 8.7–19.0 (16)] and minimum [10.0–13.6% SL (mean 12) vs 7.1–15.9 (13.7)] caudal peduncle depth, and the smaller head width [10.4–14.2% SL (mean 12) vs 11.6–14.5 (13.2)] (Table 2, Fig. 3).

Etymology

Etymology not explained in the original description. Probably, the species epithet *alberti* is derived from the name of the former ‘Parc National Albert’ (now Virunga National Park) in which the type locality is located.

Material examined

Lectotype (here designated)

DEMOCRATIC REPUBLIC OF THE CONGO • Rutshuru River, May-Ya-Moto; 5–11 Nov. 1934; de Witte leg.; MRAC 64723 ([Supplementary file SM.01](#): Fiche-209).

Paralectotype

DEMOCRATIC REPUBLIC OF THE CONGO • 1 spec.; same collection data as for lectotype; MRAC 64722 ([Supplementary file SM.01](#): Fiche-210).

Other material examined

KENYA – **Lake Victoria basin** • 1 spec., holotype of *E. cercops*; Luambwa, Nzoia River, Nyanza Province; 1960; BMNH 1960.6.7.37 • 7 specs [of 13 in lot], paratypes of *E. cercops*; same collection data as for holotype; BMNH 1960.6.7.38 to 1960.6.7.50 ([Supplementary file SM.01](#): Fiche-177 to Fiche-183).

UGANDA – **Lake Edward** • 1 spec. [of 2 in lot]; Nchwera River, Rwenshama-Ishasha road; 0°27'30.8" S, 29°48'07.0" E; 8 Nov. 2016; HIPE exped.; GenBank: MT251114; RMCA 2016.035.P.0148 to 2016.035.P.0149 ([Supplementary file SM.01](#): E31). • 1 spec. [of 2 in lot]; same collection data as for preceding; RMCA 2016.035.P.0171 to 2016.035.P.0172 ([Supplementary file SM.01](#): HP1028). • 1 spec.; Kayanja, offshore, Lake Edward; 0°05'31.2" S, 29°45'30.3" E; 20 Jan. 2018; HIPE exped.; GenBank: MT251133; RMCA 2018.008.P.0247 ([Supplementary file SM.01](#): HP2599). • 2 specs.; Nyamweru River, mouth, Kisenji; 0°18'42.5" S, 29°51'36.0" E; 31 Jan. 2018; HIPE exped.; RBINS 25585 to 25586 ([Supplementary file SM.01](#): Fiche-118, Fiche-119) – **Lake George** • 5 specs; River 2 km east of Kitongore; 0°05'45.6" S, 30°40'51.6" E; 31 Oct. 2016; HIPE exped.; GenBank: MT251105, MT251120, MT251121, MT251106, MT251107; RMCA 2016.035.P.0159 to 2016.035.P.0163 ([Supplementary file SM.01](#): HP592, HP595, HP596, HP600, HP602) • 2 specs; Mpanga River, mouth, Lake George; 0°02'20.4" N, 30°17'24.0" E; 31 Oct. 2016; HIPE exped.; GenBank: MT251119, MT251104; RMCA 2016.035.P.0164 to 2016.035.P.0165 ([Supplementary file SM.01](#): HP575, HP579) • 1 spec.; Mahoma River, Rwimi-Nyabani road; 0°21'00.2" N, 30°16'41.0" E; 1 Apr. 2017; HIPE exped.; GenBank: MT251110; RMCA 2017.006.P.0244 ([Supplementary file SM.01](#): HP1878) • 1 spec.; Lake George, Kashaka Bay, south of inlet; 0°05'04.6" S, 30°10'45.6" E; 2 Feb. 2018; HIPE exped.; GenBank: MT251111; RMCA 2018.008.P.0248 ([Supplementary file SM.01](#): HP3246) – **Kazinga Channel** • 4 specs; Kyambura River, mouth, Kazinga Channel; 0°07'25.8" S, 30°03'07.5" E; 30 Oct. 2016; HIPE exped.; GenBank: MT251100, MT251101, MT251102, MT251103; RMCA 2016.035.P.0155 to 2016.035.P.0158 ([Supplementary file SM.01](#): HP562(2), HP563 to HP565) • 7 specs; same locality; 4 Feb. 2018; HIPE exped.; RBINS 25588 to 25594 ([Supplementary file SM.01](#): Fiche-143 to Fiche-149) • 4 specs; same collection data as for preceding; GenBank: MT251099, MT251112; RMCA 2018.008.P.0249 to 2018.008.P.0252 ([Supplementary file SM.01](#): HP3312, HP3314, HP3317, HP3319) • 1 spec.; Kyambura River, middle course, north of Lake Katinda; 0°12'23.7" S, 30°06'24.3" E; 2 Feb. 2018; HIPE exped.; RBINS 25587 ([Supplementary file SM.01](#): Fiche-128) • 5 specs; Kazinga Channel, near Queen Elisabeth Bush Lodge; 0°08'09.6" S, 30°02'27.6" E; 4 Nov. 2016; HIPE exped.; GenBank: MT251123, MT251124, MT251125, MT251108, MT251109; RMCA 2016.035.P.0166 to 2016.035.P.0170 ([Supplementary file SM.01](#): HP719 to HP721, HP723, HP724) • 2 specs; Kazinga Channel, opposite of mouth Kyambura River; 0°07'17.5" S, 30°02'59.0" E; 4 Feb. 2018; HIPE exped.; RBINS 25595 to 25596 ([Supplementary file SM.01](#): Fiche-121, Fiche-123).

Description

Based on the lectotype and one paralectotype of *E. alberti*, the type series of *E. cercops*, which is synonymised here as *E. alberti*, and 37 additional specimens from the Lake Edward system, identified as *E. alberti*. The lectotype is illustrated in Fig. 7a. Maximum observed size: 74.3 mm SL. Morphometric and meristic data are given in Table 2. Body fusiform, largest depth anterior to dorsal fin. Dorsal profile from tip of snout to origin of dorsal fin slightly convex, slightly tapering to base of caudal fin. Ventral profile from operculum to origin of pelvic fin slightly convex, slightly tapering to posterior end of anal fin base, then slightly concave to caudal fin. Head small. Eye large and round, located dorso-laterally, closer to tip of snout than to distal margin of operculum, interorbital profile slightly convex. Snout rounded and mouth subterminal. Two pairs of barbels, anterior barbel usually slightly shorter than posterior with anterior one usually reaching up to vertical through posterior margin of eye, while posterior one usually up to vertical trough posterior margin of pre-operculum. Dorsal fin with 3 unbranched and 7 to 9 branched rays, distal margin straight to slightly concave, origin located slightly anterior [1 or 2 lateral

line scale(s)] to vertical through pelvic fin insertion. First branched dorsal fin ray longest, posterior rays decreasing progressively in size. Pectoral fin with 1 unbranched and 13 to 16 branched rays, distal profile straight to slightly convex, not reaching anterior base of pelvic fin. Pelvic fin with 1 unbranched and 6 to 8 branched rays, distal margin slightly convex. Anal fin with 3 unbranched and 5 to 6 branched fin rays, distal margin slightly concave. Caudal fin forked with outer rays twice as long as median ones and both lobes rounded and of similar size. Anus and urogenital opening situated immediately in front of anal fin base. Scales cycloid, rounded and radially striate. Lateral line completely pored with many lateral line scales [27–34 (median 31)], and gently curved downwards over abdomen but running straight along middle of caudal peduncle and ending at base of caudal fin. Lateral-line scales smaller on caudal peduncle than below dorsal fin.

Colour pattern

No sexual dimorphism observed. In life, overall background colour of body silvery, darker toward dorsum and lighter towards belly (Fig. 7b). Thick yellowish midlateral band, often with one to three darker spots. All fins translucent. In preserved specimens, overall background colour of body yellowish, greyish dorsally (Fig. 7a). One to three dark spots on flanks on thick silvery midlateral band; spots fused into mid-lateral line in some specimens, overlying silvery band and starting posterior to operculum. First spot situated anterior to dorsal fin origin, median one below last ray of dorsal fin and last one at caudal fin base. Specimens with more than three spots are rare (1 specimen with 4 spots and another with 6 spots).

Distribution (Fig. 10)

Enteromius alberti occurs in river systems throughout the Lake Edward basin. For the Congolese part of the basin, it is known from its type locality, the Rutshuru River, May-Ya-Moto (Poll 1939). Although the Congolese part of the system was not sampled during the recent expeditions, we identified specimens from the collection at the RMCA (86-01-P-479 to 500 and 86-09-P-70 to 71) from Vitshumbi, located in the southern Congolese part of the Lake Edward system, as *E. alberti*. In the Ugandan part, we collected the species in the Mahoma, Mpanga, Nchwera, Nyamweru and Kyambura (an affluent of the Rusangwe) Rivers, in Lake Edward offshore at Kayanja, and in Lake George at Kashaka Bay. For the Lake Victoria basin, *E. alberti* is known from the Nzoia River, the Malawa River and the Middle Akagera system (Whitehead 1960; Greenwood 1966; De Vos & Thys van den Audenaerde 1990; Seegers *et al.* 2003).

Enteromius mimus (Boulenger, 1912)

Fig. 8, Table 2

Diagnosis

Enteromius mimus (Fig. 8) belongs to the group of species of *Enteromius* with a flexible last unbranched dorsal fin ray that lacks serrations along its posterior edge. A comparison was made to other species of *Enteromius* from this group from the East Coast and Nilo-Sudan ichthyofaunal provinces (list made based on information available in, e.g., Greenwood 1962; Okaronon *et al.* 1997; Seegers *et al.* 2003; Schmidt *et al.* 2017; Froese & Pauly 2018). *Enteromius mimus* can easily be distinguished from the other species of this group from the East Coast and Nilo-Sudan ichthyofaunal regions by the following combinations of characteristics (data from original description, unless otherwise stated): a complete lateral line vs an incomplete lateral line in *E. atkinsoni*, *E. pumilus*, *E. serengetiensis*, *E. tongaensis* and *E. toppini*; two pairs of barbels vs one pair in *E. pseudotoppini*, and no barbels in *E. anema* and *E. profundus*; one to three dark spots on the flanks, which sometimes fuse into a mid-lateral line in preserved specimens, starting posterior to the operculum vs a dark line running from the tip of the snout to the caudal fin base in *E. bifrenatus* and *E. yongei*, and a thin dark line from the beginning of the operculum to the caudal fin base in *E. viviparus*; 11–12 scales around the caudal peduncle vs

8 in *E. leonensis*, 9–10 in *E. venustus*, and 10 in *E. magdalenae* and *E. yeiensis*; 24–27 lateral line scales (median 25) vs 30 in *E. lineomaculatus*, and 31 *E. innocens*; 3.5–4.5 scales between the dorsal fin base and the lateral line vs 5.5 in *E. unitaeniatus*, and 6 in *E. usambarae*; 3–4 scales between the lateral line and the pelvic fin (median 3) vs 2 in *E. trispilopleura*, and 2–2.5 in *E. neglectus* (Boulenger 1907); 7–8 branched dorsal fin rays vs 9 in *E. quadripunctatus*; a body depth which is larger than the head length vs a body depth which is equal to the head length in *E. nigeriensis*; a smaller snout length [4.1–7.1% SL (average 6.0) vs 7.1–10.1] in *E. radiatus* (Greenwood 1970). *Enteromius mimus* differs from *E. perince* by a combination of a lower number of lateral line scales [24–27 (median 25) vs 29–30 (30)], a lower number of scales between the dorsal fin base and lateral line [3.5–4.5 (median 3.5) vs 5.5], a lower number of scales around the caudal peduncle [11–12 (median 12) vs 14], a smaller interorbital width [6.3–8.3% SL (average 7.8) vs 9.8–10.2 (10.0)], a larger pre-pectoral distance [26.0–29.0% SL (average 27.4) vs 23.1–24.5 (23.8)], a lower minimum caudal peduncle depth [11.1–14.0% SL (average 12.5) vs 15.0–16.4 (15.5)], a lower maximum caudal peduncle depth [12.9–16.5% SL (average 14.6) vs 17.7–19.4 (18.8)], and a smaller anal fin base length [7.3–8.7% SL (average 8.0) vs 8.5–9.6 (9.1)]. *Enteromius mimus* differs from *E. stigmatopygus* by a combination of a smaller pre-pectoral distance [26.0–29.0 (average 27.4) vs 29.1–33.1 (30.8)], and a larger anal fin length [18.0–19.7 (average 19.0) vs 12.6–17.4 (14.8)]. *Enteromius mimus* differs from *E. alberti* by a lower number of lateral line scales [24–27 (median 25) vs 27–34 (31)], a larger pre-anal distance [68.4–74.8% SL (average 72.4) vs 65.1–73.0 (69.3)], a smaller post-anal distance [16.3–19.3% SL (average 17.8) vs 16.3–24.2 (21.1)], a larger body depth [26.5–34.3% SL (average 30.1) vs 21.7–31.2 (26.9)], a larger head depth [17.8–21.8% SL (average 20.2) vs 15.1–19.0 (17.3)] and a larger pelvic fin length [18.2–22.4% SL (average 20.4) vs 15.0–20.9 (18.0)] (Table 2). Specimens from *E. mimus* differ from the specimens of the population of *E. cf. mimus* from the Lake Edward system by a lower number of scales between the origin of the dorsal fin and the lateral line [3.5–4.5 (median 3.5) vs 3.5–4.5 (4.5)], a larger pelvic fin length [18.2–22.4% SL (average 20.4) vs 14.4–21.3 (18.5)], a smaller snout length [4.1–7.1% SL (average 6.0) vs 4.6–8.3 (7.0)], a smaller interorbital width [6.3–8.3% SL (average 7.8) vs 6.9–9.9 (8.7)], a larger post-dorsal distance [34.8–40.4% SL (average 38.1) vs 31.0–39.9 (35.9)] and a larger anal fin length [18.0–19.7% SL (average 19.0) vs 14.4–21.8 (17.7)] (Table 2).

Etymology

The specific epithet ‘*mimus*’ means ‘imitator’, a reference to the ‘striking resemblance’ to *E. neglectus* (Boulenger 1912; Scharpf & Lazara 2019).



Fig. 8. Lectotype of *Enteromius mimus* (Boulenger, 1912) (BMNH 1912.3.22.99) with 43.6 mm SL.

Material examined

Lectotype (here designated)

KENYA • Euasso Nyiro, bellow falls, British East Africa; BMNH 1912.3.22.99 ([Supplementary file SM.01](#): Fiche-185).

Paralectotypes

KENYA • 8 specs [of 9 in lot]; same collection data as for lectotype; BMNH 1912.3.22.90 to 1912.3.22.98 ([Supplementary file SM.01](#): Fiche-184, Fiche-186 to Fiche-188, Fiche-B to Fiche-E).

Description

The redescription of *E. mimus* is based on the specimens of the type series only (the lectotype and eight paralectotypes). The lectotype is illustrated in Fig. 8. Maximum observed size: 45.6 mm SL. Morphometric and meristic data are given in Table 2. Body fusiform, largest depth anterior to dorsal fin. Dorsal profile from tip of snout to origin of dorsal fin slightly convex, slightly tapering to base of caudal fin. Ventral profile from operculum to origin of pelvic fin slightly convex, slightly tapering to posterior end of anal fin base, then slightly concave to caudal fin. Head small. Eye large and round, located laterally, closer to tip of snout than distal margin of operculum, interorbital profile slightly convex. Snout rounded. Mouth subterminal. Two pairs of barbels, anterior barbel shorter than posterior with anterior one usually reaching up to vertical through the middle of the eye, while posterior one can reach the vertical trough posterior margin of pre-operculum. Dorsal fin with 3 unbranched and 7 to 8 branched rays, distal margin slightly concave, origin located on vertical through pelvic fin insertion or slightly anterior (1 lateral line scale). First branched dorsal fin ray longest, posterior rays decreasing progressively in size. Pectoral fin with 1 unbranched and 12 to 14 branched rays, distal profile straight to slightly convex, not reaching anterior base of pelvic fin. Pelvic fin with 1 unbranched and 7 branched rays, distal margin convex. Anal fin with 3 unbranched and 5 to 6 branched fin rays, distal margin concave. Caudal fin forked with outer rays twice as long as median ones and both lobes rounded and of similar size. Anus and urogenital opening situated immediately in front of anal fin base. Scales cycloid rounded and radially striate. Lateral line completely pored with many lateral line scales (total) [24–27 (median 25)], gently curved downwards over abdomen but running straight along middle of caudal peduncle and ending at base of caudal fin.



Fig. 9. Fresh specimen of *E. cf. mimus* (Boulenger, 1912) (RMCA 2016.035.P.0125-0139 HP547) with 45.2 mm SL.

Colour pattern

No sexual dimorphism is observed. No information of in vivo colour pattern is available. In preserved specimens, overall background colour of body brown, darker dorsally. One to three dark spots on flanks on thick silvery midlateral band; spots fused into mid-lateral line in some specimens, overlying silvery band and starting posterior to operculum. First spot situated anterior to dorsal fin origin, median one below or somewhat anterior to last ray of dorsal fin and last one at caudal fin base.

Distribution

Enteromius mimus is known from its type locality, the Euasso Nyiro River below the falls, east of Lake Baringo, Kenya, and from the Tana River system (Seegers *et al.* 2003). For the time being, the specimens of the Lake Edward system are referred to as *E. cf. mimus* and are not included in the distribution of *E. mimus*.

Discussion

Enteromius alberti and *Enteromius cf. mimus*

Although the occurrence of *E. perince* and *E. stigmatopygus* in the Lake Edward system was mentioned in several studies (e.g., Poll 1939; Greenwood 1966; Decru *et al.* 2019), we found that the specimens from the Lake Edward system, previously assigned to these species, clearly differed from the syntypes of these species in morphology. The genetic distance between the specimens from the Lake Edward system and sequences of *E. perince* from GenBank was large (12%). Based on our study, we can conclude that *E. perince* and *E. stigmatopygus* do not occur in the system. Instead, the specimens of *Enteromius* from the Lake Edward system with a smooth unbranched dorsal fin ray are assigned to either *E. alberti* (“group A”) or *E. cf. mimus* (“group B”), which share a very similar colour pattern. However, no correspondence was found between specimens previously identified as *E. stigmatopygus* or *E. perince* and their current identification as *E. alberti* or *E. cf. mimus*. Specimens from the system, which were historically assigned to *E. stigmatopygus*, include both specimens of *E. alberti* and *E. cf. mimus*. The same applies to specimens historically assigned to *E. perince*.

Banister (1987) considered *E. alberti* to be a synonym of *E. stigmatopygus*, although he did not examine the syntypes of *E. alberti*. The synonymy was based on a similar position of the gill rakers, the alignment of pharyngeal tooth rows and the position of the flank spots. However, the number of lateral line scales was different (Banister, 1987); 24 to 26 in *E. stigmatopygus*, according to Banister (1987), compared to 31 in *E. alberti*, according to Poll (1939). We found similar differences in the present study: *E. alberti* has 27 to 34 and the type series of *E. stigmatopygus* has 20 to 25 lateral line scales. Furthermore, in the original description of *E. stigmatopygus*, Boulenger (1903) mentioned that the syntypes had no barbels. However, Banister (1987) found one pair of posterior barbels in the three largest syntypes, and no sign of anterior barbels, but at the same time emphasized the poor condition of these syntypes. Also in the present study, we did not find distinct anterior barbels. Posterior barbels were found in the larger type specimens of *E. stigmatopygus*. In his redescription, Banister (1987) included additional specimens (amongst which the types of *E. alberti*) and stated that the anterior barbels appear later in development. The two pairs of barbels in *E. alberti* are clearly visible.

In the present study, we found the holotype and the examined paratypes of *E. cercops* to be conspecific with *E. alberti*. *Enteromius cercops* was described in 1960 from the Nzoia River (Nyanza Province, Kenya, Lake Victoria basin) by Whitehead. In addition to its type locality, *E. cercops* is also known from other rivers in the Lake Victoria basin, such as the Malawa River (Uganda) and rivers in the Middle Akagera system (Rwanda) (Whitehead 1960; Greenwood 1966; De Vos & Thys van den Audenaerde 1990; Seegers *et al.* 2003). We revalidated *E. alberti* with *E. cercops* as its junior synonym.

We found the specimens of “group B” to be most similar to *E. mimus*. The syntypes of *E. mimus* originated from the Euasso Nyiro River (Kenya), which drains to the Indian Ocean and is situated further east in the East Coast ichthyofaunal province (Fig. 10). Furthermore, *E. mimus* is only known from this type locality and from the Tana River system (Seegers *et al.* 2003). The type series of *E. mimus* is polyspecific as it included a specimen with serrations on the third unbranched dorsal fin ray (not included in the analyses), though Boulenger (1912) clearly mentioned the lack of serrations as a feature of the species. Further comparative research on the species of *Enteromius* from the coastal river systems in Kenya is required in order to identify this specimen. Since some small differences were observed between “group B” and *E. mimus* in the results of the PCA on the measurements (Fig. 6, Table 2), we assigned “group B” to *E. cf. mimus*, with “cf.” indicating specimens that are comparable to *E. mimus* but whose identification is uncertain (Decru *et al.* 2016). Furthermore, “group B” and *E. mimus* occur in distant river systems. Therefore, it is unlikely that the specimens of the Lake Edward system are conspecific with the geographical distant species *E. mimus*, though this possibility

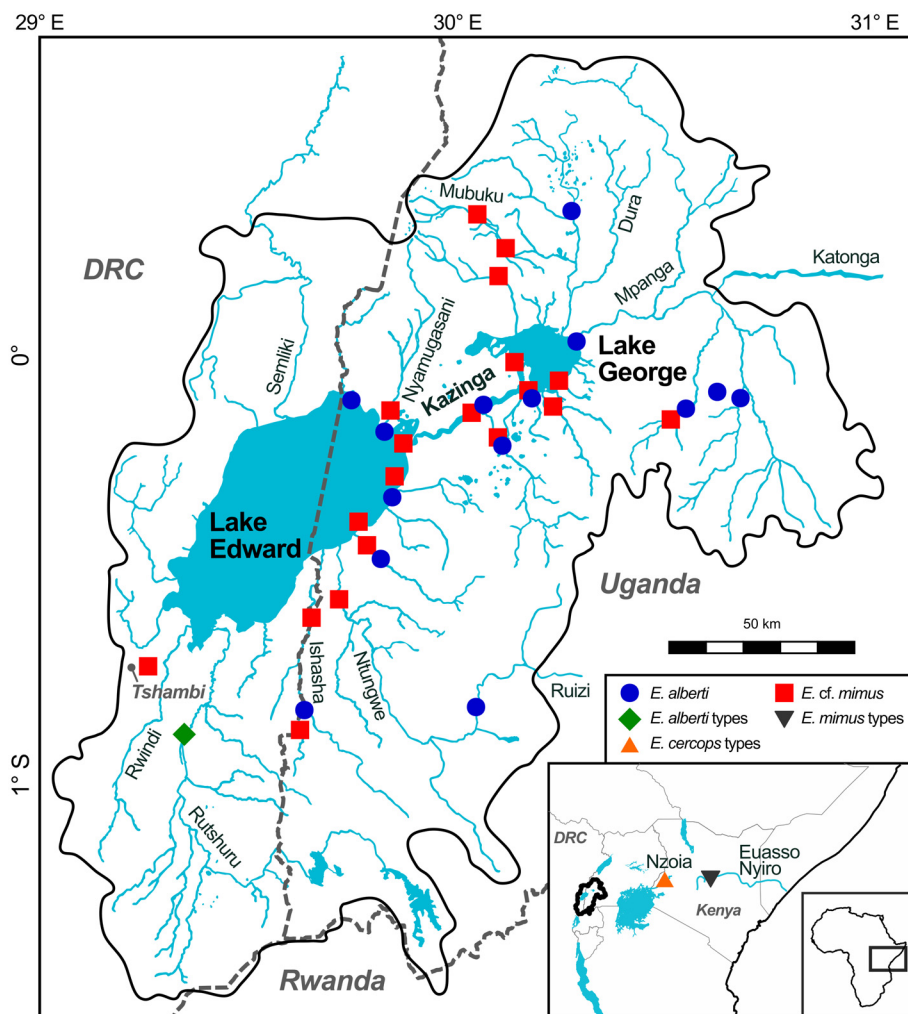


Fig. 10. Overview of the sample locations of *E. alberti* (Poll. 1939) (●) and *E. cf. mimus* (Boulenger, 1912) (■), including the specimens from Tshambi, in the Lake Edward system. The location of the lectotype and the paralectotypes of *E. alberti* (◆). The approximate location of the lectotype and the paralectotypes of *E. mimus* (Boulenger, 1912) (▼) and the holotype and paratypes of *E. cercops* (Whitehead, 1960) (▲) are indicated in the inset.

cannot be excluded. Genetic studies already revealed that widespread species of *Enteromius* often consist of multiple species that are actually confined to smaller distribution areas (Schmidt *et al.* 2017; Van Ginneken *et al.* 2017). While we found *E. perince* and *E. stigmatopygus* not to occur in the Lake Edward system, it is remarkable that we found a comparable set of similarly looking species in this system: *E. alberti* and *E. cf. mimus*, which mirror *E. perince* and *E. stigmatopygus* in the Nile River. Whether or not this implies sister-group relationships between species of *Enteromius* of the two ichthyofaunal provinces, is difficult to say without a more comprehensive genetic study. Furthermore, COI data of *E. stigmatopygus* is lacking. The occurrence of sister relationships between other species of *Enteromius* from the East Coast and other ichthyofaunal provinces has been suggested by Ndeda *et al.* (2018). These authors found sister relationship between *E. yongei* (from Lake Victoria, East Coast) and a lineage containing a specimen identified as *E. sp.* (region of Conakry) and one as *E. stigmatopygus* (Mafou River, Niger River) with a 12% genetic divergence in the cytochrome b (Cytb) gene (mtDNA). However, in view of the small sample size, especially of the West African lineage, the vast geographical distance and the use of only one mitochondrial marker, these results need further confirmation.

Unknown diversity in *Enteromius*

In a recent study on species of *Enteromius* from the north-eastern part of the Congo basin (Van Ginneken *et al.* 2017), DNA barcodes (COI) indicated the presence of 23 mitochondrial lineages within what initially were assumed to be only four different morphospecies. Genetic distances were mostly well over 5% and even up to 20% between lineages of morphologically similar specimens, clearly exceeding 2% which is the cut-off value that is commonly used to denote intraspecific variation (Hebert *et al.* 2003). In the study of Van Ginneken *et al.* (2017), clear-cut diagnostic characteristics could, however, not be delineated. Yet, morphologic differences could be demonstrated with multivariate morphometric analyses, which were consistent with the COI lineages. This unrecognised diversity was explained by the occurrence of a cryptic diversity within the species from the Congo basin. In the present study, we found seven characteristics to distinguish the two morphologically similar species of the Lake Edward system. Hence, although, a priori, we failed to distinguish the two species from each other, the concept of cryptic species is not applicable here. Another study (Schmidt *et al.* 2019) also revealed unrecognised diversity in *E. foutensis* from the Fouta Djallon (Upper Guinea region) highlands, both genetically (Cytb) and morphologically. Schmidt *et al.* (2017) also found evidence of high levels of genetic divergence and unrecognised diversity (Cytb) in specimens identified as *E. kerstenii*, *E. apleurogramma* and *E. cf. paludinosus* from the East Coast ichthyofaunal province in Kenya. Also, patterns of introgression seem to occur in both closely and distantly related species of *Enteromius* (Schmidt *et al.* 2017), which suggest hybridisation events. Whether this is also the case in the specimens of *E. alberti* and *E. cf. mimus* remains to be studied.

The results of these recent integrative studies on other systems raised the expectation to find more species in the Lake Edward system as well. This was, however, not the case for the group with an unbranched third dorsal fin ray. Initially, two species, though misidentified, were reported for this group, and during the present study no additional species were found.

The unrecognised diversity found within species complexes in various systems (e.g., Schmidt *et al.* 2017, 2019; Van Ginneken *et al.* 2017), the revalidation of species as found in our study and the study of Schmidt *et al.* (2018), and the description of new species, such as *E. pinnimaculatus* from Gabon (Mipounga *et al.* 2019) and *E. thespesios* from the Upper Congo River (Katemo Manda *et al.* 2019) all suggest that the species richness of *Enteromius* is much larger than currently thought. Hence, the present number of 211 valid species of *Enteromius* (Froese & Pauly 2019), is certainly a considerable underestimation of the real species diversity.

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References

- Bamba M. 2012. *The ‘Barbus’ species (Cypriniformes, Cyprinidae) from Côte d’Ivoire: A systematic revision of some West African species complexes*. PhD Tesis, KU Leuven, Belgium.
- Bamba M., Vreven E.J. & Snoeks J. 2011. Description of *Barbus teugelsi* sp. nov. (Cypriniformes: Cyprinidae) from the Little Scarces basin in Guinea, Africa. *Zootaxa* 2998: 48–65. <https://org/10.11646/zootaxa.2998.1.4>
- Banister K.E. 1987. The *Barbus perince*-*Barbus neglectus* problem and a review of certain Nilotic small *Barbus* species (Teleostei, Cypriniformes, Cyprinidae). *Bulletin of the Natural History Museum, Zoology series* 53 (2): 115–138.
- Berrebi P., Kottelat M., Skelton P. & Rab P. 1996. Systematics of *Barbus*: state of the art and heuristic comments. *Folia Zoologica* 45: 5–12.
- Bookstein F., Chernoff B., Elder R., Humphries J., Smith G. & Strauss R. 1985. Morphometrics in Evolutionary Biology: the geometry of size and shape change, with examples from fishes. *Journal of the Academy of Natural Sciences of Philadelphia, Special publication* 15: 1–277.
- Boulenger G.A. 1903. Diagnosis of four new species of *Barbus* from the Nile. *Annals and Magazine of Natural History, Series 7* 12: 532–533. <https://doi.org/10.1080/00222930308678890>
- Boulenger G.A. 1907. *Zoology of Egypt: the Fishes of the Nile*. Published for the Egyptian Government by Hugh Rees, London. <https://doi.org/10.5962/bhl.title.51710>
- Boulenger G.A. 1912. On a collection of Fishes made by Mr. A. Blayney Percival in British East Africa to the East of Lake Baringo. *Proceedings of the Zoological Society of London* 82 (3): 672–676. <https://doi.org/10.1111/j.1469-7998.1912.tb07548.x>
- Boulenger G.A. 1916. *Catalogue of the Fresh-Water Fishes of Africa in the British museum (Natural History), Vol. IV*. British Museum (Natural History), London, UK. <https://doi.org/10.5962/bhl.title.8869>
- Clark K., Karsch-Mizrachi I., Lipman D.J., Ostell J. & Sayers E.W. 2016. GenBank. *Nucleic Acids Research* 44 (D1): D67–D72. <https://doi.org/10.1093/nar/gkv1276>
- De Vos L. & Thys van den Audenaerde D.F.E. 1990. Petit *Barbus* (Pisces, Cyprinidae) du Rwanda. *Revue d’Hydrobiologie tropicale* 23 (2): 141–159.

- Decru E., Vreven E. & Snoeks J. 2012. A revision of the West African *Hepsetus* (Characiformes: Hepsetidae) with a description of *Hepsetus akawo* sp. nov. and a redescription of *Hepsetus odoe* (Bloch, 1794). *Journal of Natural History* 46: 1–23. <https://doi.org/10.1080/00222933.2011.622055>
- 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. <https://doi.org/10.1111/1755-0998.12445>
- 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 Fish Biology* 96 (5): 1186–1201. <https://doi.org/10.1111/jfb.13992>
- Froese R. & Pauly D. (eds) 2018. FishBase. Available from www.fishbase.org [accessed 21 Nov. 2018].
- Froese R. & Pauly D. (eds) 2019. FishBase. Available from www.fishbase.org [accessed 6 Nov. 2019].
- Greenwood P.H. 1962. A revision of certain *Barbus* (Pisces, Cyprinidae) from East, Central and South Africa. *Bulletin of the Natural History Museum, Zoology series* 8 (4): 151–208. Available from <https://www.biodiversitylibrary.org/part/118628#/summary> [accessed 21 Nov. 2018].
- Greenwood P.H. 1966. *The Fishes of Uganda*. The Uganda Society, Kampala.
- Greenwood P.H. 1970. A revision of the cyprinid species *Barbus* (*Enteromius*) *radiatus* Peters, 1853, with a note on the synonymy of the subgenera *Beirabarus* and *Enteromius*. *Revue de Zoologie et de Botanique africaines* 82: 1–13.
- Hayes M.M. & Armbruster J.W. 2017. The taxonomy and relationships of the African small barb (Cypriniformes: Cyprinidae). *Copeia* 105 (2): 348–362. <https://doi.org/10.1643/CI-15-348>
- Hebert P.D.N., Cywinska A., Ball S.L. & deWaard J.R. 2003. Biological identifications through DNA barcodes. *Proceedings of the Royal Society of London B. Biological Sciences* 270: 313–321. <https://doi.org/10.1098/rspb.2002.2218>
- Howes G.J. 1991. Systematics and biogeography: an overview. In: Winfield I.J. & Nelson J.S. (eds) *Cyprinid Fishes: Systematics, Biology and Exploitation*: 1–33. Chapman & Hall, London, UK.
- 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>
- Kassambara A. & Mundt F. 2017. Factoextra: extract and visualize the results of multivariate data analyses. R package version 1.0.5. Available from <https://CRAN.R-project.org/package=factoextra> [accessed 1 Apr. 2020].
- Katemo Manda B., Snoeks J., Decru E., Bills R. & Vreven E. 2019. *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>
- 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>
- Leigh J.W. & Bryant D. 2015. POPART: full-feature software for haplotype network construction. *Methods in Ecology and Evolution* 6: 1110–1116. <https://doi.org/10.1111/2041-210X.12410>
- Levin B.A., Dgebuadze Y.Y., Tefera F., Tesfaye G. & Golubtsov A.S. 2017. An evidence of past introgressive hybridization between *Labeobarbus ethiopicus* and *L. intermedius* in the Ethiopian Rift Valley, East Africa. *Ethiopian Journal of Biological Sciences* 16 (Suppl.): 45–60.
- Lowe-McConnell R.H. 1975. *Fish Communities in Tropical Freshwaters*. Longman, New York, USA.

- Manly B.F.J. 1994. *Multivariate Statistical Methods: A Primer*. 2nd Ed. Chapman & Hall, Boca Raton, Florida, USA.
- Mbalassa M., Bagalwa J.J.M., Nshombo M. & Kateyo M.E. 2014. Assessment of physicochemical parameters in relation with fish ecology in Ishasha River and Lake Edward, Albertine Rift Valley, East Africa. *International Journal of Current Microbiology and Applied Sciences* 3(6): 230-244.
- Mipounga H.K., Cutler J., Beh J.H.M., Adam B. & Sidlauskas B.L. *Enteromius pinnimaculatus* sp. nov. (Cypriniformes: Cyprinidae) from southern Gabon. *Journal of Fish Biology* 96 (5): 1218–1233. <https://doi.org/10.1111/jfb.13995>
- Ndeda V.M., Mateos M. & Hurtado L. 2018. Evolution of African barbs from the Lake Victoria drainage system, Kenya. *PeerJ* 6: e5762. <https://doi.org/10.7717/peerj.5762>
- Nelson J.S., Grande T.C. & Wilson M.V.H. 2016. *Fishes of the World*. 5th Ed. John Wiley & Sons, Hoboken, New Jersey. <https://doi.org/10.1002/9781119174844>
- Okaronon J.O., Katunzi E.F.B. & Asila A.A. 1997. *Fish Species Identification Guide for Lake Victoria, Enumerator's Field Guide*. Lake Victoria Fisheries Research Project Phase II, Technical Document 1, Jinja, Uganda. Available from <http://aquaticcommons.org/4150/> [accessed 21 Nov. 2018].
- Oksanen J., Blanchet F.G., Friendly M., Kindt R., Legendre P., McGlenn D., Minchin P.R., O'Hara R.B., Simpson G.L., Solymos P., Stevens M.H.H., Szoecs E. & Wagner H. 2018. Vegan: Community Ecology Package. R package version 2.5-2. Available from <https://CRAN.R-project.org/package=vegan> [accessed 31 Aug. 2019].
- Poll M. 1939. Poissons. *Exploration du Parc National Albert. Mission G.F. de Witte (1933-1935)* fasc. 24: 1–81. Available from <http://www.apncb.be/missions/mission-scientifique-au-parc-national-albert-de> [accessed 8 Jun. 2018].
- R Core Team. 2018. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. Available from <https://www.R-project.org/> [accessed 29 Feb. 2020].
- 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>
- 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>
- Roberts T.R. 1975. Geographical distribution of African freshwater fishes. *Zoological Journal of the Linnean Society* 57: 249–319. <https://doi.org/10.1111/j.1096-3642.1975.tb01893.x>
- RStudio Team. 2016. *RStudio: Integrated Development for R*. RStudio Inc., Boston, MA. Available from <http://www.rstudio.com/> [accessed 3 Jul. 2020].
- Scharpf C. & Lazara K.J. 2019. The ETYFish Project. Available from www.etyfish.org [accessed 17 Sep. 2019].
- Schmidt R.C., Bart Jr. H.L. & 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>
- Schmidt R.C., Bart Jr. H.L. & Nyingi W.D. 2018. Integrative taxonomy of the red-finned barb, *Enteromius apleurogramma* (Cyprininae: Smiliogastrini) from Kenya, supports recognition of *E. amboseli* as a valid species. *Zootaxa* 4482 (3): 566–578. <https://doi.org/10.11646/zootaxa.4482.3.8>

- Schmidt R.C., Dillon M.N., Kuhn N.M., Bart Jr. H.L. & Pezold F. 2019. Unrecognized and imperilled diversity in an endemic barb (Smiliogastrini, *Enteromius*) from the Fouta Djallon highlands. *Zoologica Scripta* 48 (5): 605–613. <https://doi.org/10.1111/zsc.12362>
- Schwarzer J., Swartz E.R., Vreven E., Snoeks J., Cotterill F.P.D., Misof B. & Schliewen U.K. 2012. Repeated trans-watershed hybridization among haplochromine cichlids (Cichlidae) was triggered by Neogene landscape evolution. *Proceedings of the Royal Society of London B. Biological Sciences* 279 (1746): 4389–4398. <https://doi.org/10.1098/rspb.2012.1667>
- Seegers L., De Vos L. & Okeyo D.O. 2003. Annotated checklist of the freshwater fishes of Kenya (excluding the lacustrine haplochromines from Lake Victoria). *Journal of East African Natural History* 92: 11–47. [https://doi.org/10.2982/0012-8317\(2003\)92%5B11:ACOTFF%5D2.0.CO;2](https://doi.org/10.2982/0012-8317(2003)92%5B11:ACOTFF%5D2.0.CO;2)
- Seehausen O. & Wagner C.E. 2014. Speciation in freshwater fishes. *Annual Review of Ecology, Evolution, and Systematics* 45: 621–651. <https://doi.org/10.1146/annurev-ecolsys-120213-091818>
- Skelton P.H. 1994. Diversity and distribution of freshwater fishes in East and Southern Africa. *Annals of the Royal Central Africa Museum (Zoology)* 275: 95–131.
- Skelton P.H., Tweddle D. & Jackson P.B.N. 1991. Cyprinids of Africa. In: Winfield I.J. & Nelson J.S. (eds) *Cyprinid Fishes: Systematics, Biology and Exploitation*: 211–239. Chapman & Hall, London, UK.
- Snoeks J. 2004. *The Cichlid Diversity of Lake Malawi/Nyasa/Niassa: Identification, Distribution and Taxonomy*. Cichlid Press, El Paso, USA.
- Snoeks J., Harrison I.J. & Stiassny M.L.J. 2011. The status and distribution of freshwater fishes. In: Darwall W.R.T., Smith K.G., Allen D.J., Holland R.A., Harrison I.J. & Brooks E.G.E. (eds) *The Diversity of Life in African Freshwaters: Under Water, Under Threat. An Analysis of the Status and Distribution of Freshwater Species throughout Mainland Africa*: 42–73. IUCN, Cambridge & Gland.
- Templeton A.R., Crandall K.A. & Sing C.F. 1992. A cladistic analysis of phenotypic associations with haplotypes inferred from restriction endonuclease mapping and DNA sequence data. III. Cladogram estimation. *Genetics* 132: 619–633.
- 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>
- Wagner C.E., McCune A.R. & Lovette I.J. 2012. Recent speciation between sympatric Tanganyikan cichlid colour morphs. *Molecular Ecology* 21: 3283–3292. <https://doi.org/10.1111/j.1365-294X.2012.05607.x>
- Whitehead P.J.P. 1960. Three new cyprinid fishes of the genus *Barbus* from the Lake Victoria basin. *Revue de Zoologie et de Botanique africaines* 62 (1–2): 106–119.
- Yang L., Sado T., Hirt M.V., 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>

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Supplementary files

SM.01. Overview of the specimens used for morphological and genetic analyses.

SM.02. PC loadings and percentages of total variance of the PCA on 24 log-transformed measurements of *Enteromius* Cope, 1867: group A (n = 21) and group B (n = 50).

SM.03. PC loadings and percentages of total variance of the PCA on 24 log-transformed measurements of *Enteromius* Cope, 1867 (n = 69).

SM.04. PC loadings and percentages of total variance of the PCA on 15 meristics of *Enteromius* Cope, 1867 (n = 62).

SM.05. PC loadings and percentages of total variance of the PCA on 24 log-transformed measurements of *Enteromius* Cope, 1867 (n = 105).

SM.06. PC loadings and percentages of total variance of the PCA on 15 meristics of *Enteromius* Cope, 1867 (n = 95).

SM.07. PC loadings and percentages of total variance of the PCA on 24 log-transformed measurements of *Enteromius* Cope, 1867 (n = 83).