

# The *Cyphomyrus* Myers 1960 (Osteoglossiformes: Mormyridae) of the Lufira basin (Upper Lualaba: DR Congo): A generic reassignment and the description of a new species

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## Abstract

Within a comparative morphological framework, *Hippopotamyrus aelsbroeckii*, only known from the holotype originating from Lubumbashi, most probably the Lubumbashi River, a left bank subaffluent of the Luapula River, is reallocated to the genus *Cyphomyrus*. This transfer is motivated by the fact that *H. aelsbroeckii* possesses a rounded or vaulted predorsal profile, an insertion of the dorsal fin far anterior to the level of the insertion of the anal fin, and a compact, laterally compressed and deep body. In addition, a new species of *Cyphomyrus* is described from the Lufira basin, *Cyphomyrus lufirae*. *Cyphomyrus lufirae* was collected in large parts of the Middle Lufira, upstream of the Kyubo Falls and just downstream of these falls in the lower Lufira and its nearby left bank affluent, the Luvilombo River. The new species is distinguished from all its congeners, that is, firstly, from *C. macrops*, *C. psittacus* and *C. wilverthi*, by a low number of dorsal fin rays, 27–32 (vs. higher, 36 (37), 34 (33–41) and 38 (38–40), respectively) and, secondly, from *C. aelsbroeckii*, *C. cubangoensis*, and *C. discorhynchus* by a large prepelvic distance, 41.0–43.8%  $L_S$  (vs. shorter, 39.7%, 38.9–39.1% and 37.0–41.0%  $L_S$ , respectively). The description of yet another new species for the Upemba National Park and the Kundelungu National Park further highlights their importance for fish protection and conservation in the area. Hence, there is an urgent need for the full integration of fish into the management plans of these parks.

## KEYWORDS

*Cyphomyrus aelsbroeckii*, *Cyphomyrus discorhynchus*, DNA barcoding, Kundelungu National Park, morphometry, Upemba National Park

## 1 | INTRODUCTION

The family Mormyridae is endemic to the freshwaters of Africa (Lévêque *et al.*, 1990). With a total of 224 valid species (Fricke *et al.*, 2019) and 21 genera (Sullivan *et al.*, 2016) it is one of the largest fish families on the continent. The family is present and well-diversified in most continental aquatic ecosystems (Hopkins *et al.*, 2007; Lavoué *et al.*, 2000; N'da *et al.*, 2014), with the greatest species-level diversity occurring in the Congo and Lower Guinea ichthyofaunal provinces (Hopkins *et al.*, 2007; Roberts, 1975; Sullivan *et al.*, 2016). Species of

this family are African osteoglossomorph fishes of great interest for their ability to produce electric discharges from an electric organ located in their caudal peduncle (Hopkins, 1986; Lavoué *et al.*, 2000). The highest densities of electroreceptors are on the tip of the chin, with median densities on the nasal region and low densities on the back (Hollmann *et al.*, 2008: Figure 8). The electric discharges produced are only a few millivolts and thus are not generated for attack or defence as in Malapteruridae (Skelton, 1996; Sullivan *et al.*, 2016). Instead, they are used primarily in electro-location of objects in their environment and communication, which is important for facilitating

activity at night or in murky waters (Feulner *et al.*, 2009; Hopkins, 1986; Rich *et al.*, 2017; Teugels *et al.*, 2001). Each species has its own unique electric organ discharge (EOD) and the sexes of some species also may have different discharges (Rich *et al.*, 2017).

The genus *Cyphomyrus* Myers 1960 is morphologically characterized by: (a) a rounded or arched back; and (b) a long dorsal fin, with its origin situated in between the pelvic- and the anal-fin origin and its posterior end situated behind that of the anal fin (Kramer & Van der Bank, 2011; Levin & Golubtsov, 2018; Skelton, 1996). In addition, species of *Cyphomyrus* possess 27–40 rays on the dorsal fin, 22–27 rays on the anal fin, 10–12 rays on the pectoral fin, 12, rarely 13, circumpenduncular scales (Kramer & Van der Bank, 2011; Skelton, 1996) and 58–74 scales along the lateral line (Boulenger, 1909). The chin has a short bulbous protuberance, which hides the essentially inferior position of the mouth (Kramer & Van der Bank, 2011). Teeth, generally three to five in the upper jaw and five to six in the lower jaw, are situated on the ventral midline of both jaws. The body is compact, laterally compressed and deep.

The name *Cyphomyrus* is derived from the Greek prefix '*kuphos*', meaning hunchback, and the Greek '*muros*', the often-used combining form for *mormyrus* (Myers, 1960). The genus *Cyphomyrus* currently contains six valid species (Fricke *et al.*, 2019; Kramer & Van der Bank, 2011; Levin & Golubtsov, 2018). Four of these are known from the Congo basin, more precisely *C. discorhynchus* (Peters 1852), *C. macrops* (Boulenger 1909), *C. psittacus* (Boulenger 1897) and *C. wilverthi* (Boulenger 1898) (see Gosse, 1984). *Cyphomyrus macrops* and *C. wilverthi* are Congo basin endemics (Gosse, 1984), while *C. psittacus*, described from the Wagenia or Boyoma Rapids near Kisangani (Democratic Republic of the Congo), is also found in West Africa (Bigorne, 2003; Gosse, 1984) and *C. discorhynchus*, described from the Lower Zambezi (Mozambique), is found throughout the Zambezi and the Lake Malawi and Tanganyika basins (Gosse, 1984; Scott *et al.*, 2006; Skelton, 1996). Furthermore, *C. petherici* (Boulenger 1898) is known from the White Nile, the Blue Nile, the Murchison Nile and the Omo system (Golubtsov & Darkov, 2008; Levin & Golubtsov, 2018). As such, its presence in the Congo basin, that is, the Malagarazi River (De Vos *et al.*, 2001), seems doubtful and requires confirmation (see Levin & Golubtsov, 2018). Finally, *C. cubangoensis* (Pellegrin 1936), is known from the Okavango River basin (syntypes) and Okavango delta, the Kwando River and the Upper Zambezi River system (Kramer & Van der Bank, 2011).

During a series of recent field expeditions (2012–2016), in the Upper Lualaba (*sensu* Teugels & Thieme, 2005), covering parts of both the Upemba National Park (UNP) and the Kundelungu National Park (KNP), two groups of *Cyphomyrus* specimens were collected. Of the two groups of specimens collected, the first is here identified as *C. discorhynchus*, to date the only species reported from the Upper Lualaba and the lower stretch of its largest right bank tributary, the (Lower) Lufira (see Poll, 1976). The second group consists of specimens collected in the Middle Lufira basin and just downstream of the Kyubo Falls in the Lower Lufira and the lower stretch of its nearby left bank affluent the Luvilombo River. These specimens were revealed to be morphologically clearly different from all valid *Cyphomyrus* species currently known from the Congo basin, although they are similar to *C. discorhynchus* and *Hippopotamyrus aelsbroecki* (Poll 1945), herein transferred to the genus

*Cyphomyrus* (see below). Furthermore, a detailed comparison of the newly collected specimens with *C. cubangoensis* and *C. discorhynchus*, the two species currently known from Southern Africa, was also undertaken and revealed that the specimens from the Middle and Lower Lufira represent a new species for science.

In addition, the paper also proposes the transfer of *H. aelsbroecki*, originally described as a new *Gnathonemus* from Lubumbashi, most probably the Lubumbashi River, which is a left bank subaffluent of the Luapula River, to the genus *Cyphomyrus*. This reallocation is motivated based on the external morphological diagnostic characters of the genus *Cyphomyrus* as identified by Kramer and Van der Bank (2011). As such, the purpose of the present paper is to (a) motivate the transfer of *H. aelsbroecki* to the genus *Cyphomyrus* and (b) formally describe a new *Cyphomyrus* species for science, named *C. lufirae* sp. nov.

## 2 | MATERIALS AND METHODS

### 2.1 | Collections

Specimens for this study were collected during recent field trips (2012–2016) and mostly deposited in the Royal Museum for Central Africa (RMCA) or were obtained from the Musée National d'Histoire Naturelle (MNHN), RMCA, Zoologisches Museum Berlin (ZMB) and Zoologisches Staatssammlung München (ZSM) collections. During these recent field trips, fish were caught using various fishing methods, e.g., gill nets and fykes. Freshly caught fish were anaesthetized by an overdose of clove oil. After death, fin clips for molecular analysis were taken and preserved in 99% ethanol. Specimens for further morphological studies were preserved in 10% formalin before being transferred to 70% ethanol for long-term storage at the RMCA. Permanent tags were attached to specimens bearing a unique number by which a specimen and its fin clip are linked.

### 2.2 | Morphological data

A total of 90 specimens of *Cyphomyrus* were examined, including 64 from the Upper Lualaba basin and 26 specimens from other areas for comparative purposes (see material examined). Among the 64 specimens from the Upper Lualaba basin, there were 19 specimens from the Kamalondo Depression and the more downstream part of the Lower Lufira, here all identified as *C. discorhynchus*. These specimens were included in the analyses because of the close similarity of *C. discorhynchus* with the new species and the widespread geographical distribution of this species (see Skelton, 1996). The other 45 specimens from the Upper Lualaba basin were collected from the Lower and the Middle Lufira basin, and all belong to the new species. The 26 specimens studied for comparative purposes include the lectotype and the four paralectotypes of *C. discorhynchus*. To date, *C. discorhynchus* contains two junior synonyms, *C. smithersi* (Määr 1962) and *C. tanganicanus* (Boulenger 1906). Therefore, the three syntypes of *C. tanganicanus*, originally described from Sumbu and a river at Msamba on the Lake

Tanganyika basin, and seven additional specimens, all originating from some Lake Tanganyika tributaries, were included in the analysis. Note that throughout the presentation of the results the syntypes of *C. tanganicus* and the *C. discorhynchus* specimens from the affluent rivers of the Lake Tanganyika basin have been labelled separately to illustrate the observed (geographical) differences with the *C. discorhynchus* identified specimens from the Zambezi and the Upper Lualaba. The holotype of *C. smithersi* (NMBZ 0833) could not be examined because it could not be obtained on loan. Therefore, five specimens from Lake Kariba, type locality of *C. smithersi*, were included as topotypic specimens for this species. Finally, four of the 14 syntypes of *C. cubangoensis* and the holotype of *C. aelsbroecki* were also included.

Eleven counts and 29 measurements were taken on each specimen. Counts follow Boden *et al.* (1997). For the dorsal- and anal-fin ray counts the two simple rays preceding the segmented rays were also included in these counts. All rays were counted at their base. The total number of vertebrae was not used for the analyses because it was not taken on all specimens and all species. All measurements were taken according to Boden *et al.* (1997) except for the two different measurements of the caudal peduncle depth for which only the middle caudal peduncle depth has been taken as both measurements revealed to be highly similar. Five measurements have been added, four according to Kramer and Van der Bank (2011: Figure 3): (a) the post-dorsal distance (pD), (b) the distance between pectoral and pelvic fins (PPF), (c) the length of snout 2 (LS<sub>o</sub>) and (d) the length of snout 3 (LS<sub>c</sub>). In addition, one is taken for the first time, that is the body depth at the level of the anterior insertion point of the dorsal fin, which is the distance between the anterior insertion point of the dorsal fin and the corresponding point on the ventral edge of the body when following a vertical line perpendicular on the horizontal body axis. All measurements were taken using callipers of 0.1 mm precision on the left-hand side of the specimens except when this side was damaged in which case the use of the right-hand side was mandatory.

Data were explored and analysed using multivariate principal component analyses (PCA). Meristics and measurements were analysed separately, with the correlation matrix used for the PCA on the raw meristics, and the covariance matrix for the PCA on the measurements expressed as percentages (Bookstein *et al.*, 1985). Measurements on the head were expressed in percentage of head length ( $L_H$ ) and measurements on the body in percentage of standard length ( $L_S$ ). Scatterplots were used to explore the characters that could separate the species. Statistical analyses were executed in STATISTICA software for Windows version 7 (Statsoft, Inc). Being invariable, the number of pelvic-fin rays was not included in the PCA.

In the description of the new species, measurements are expressed as proportions following Boulenger (1898) in order to allow direct comparison with the original descriptions and recent redescriptions (see Kramer & Van der Bank, 2011) of its congeners. In addition, tabulated measurements are provided in percentages alongside the description. In the diagnosis for the new species, the provided meristic comparative data for its congeners are based on: (a) first-hand personal observations; and (b) the original descriptions of these species (between brackets). This approach has been preferred to avoid reporting large amounts of meristic intraspecific variation which might be largely due to

misidentifications of subsequently collected specimens. However, for the measurements only morphometric data generated within the framework of the present study were presented, as the original descriptions lack data on the diagnostic measurements retained.

Non-parametric Mann–Whitney U-tests with sequential Bonferroni correction (Rice, 1989) were used for univariate comparisons of the raw meristic data and the percentages, in %  $L_H$  or %  $L_S$  for the head and body measurements, respectively. For measurements, specimens of similar length classes ( $96 < L_S \leq 163$ ) were used to prevent the potential confounding effects of allometric growth.

All locality data have been translated into English. Following the new policy of the RMCA, collection numbers MRAC A0–A9 are listed as MRAC 2000–2009 and B0–B6 as MRAC 2010–2016.

## 2.3 | Molecular data

For a total of 22 samples, 651 bp of the barcode gene cytochrome oxidase (COI) mitochondrial DNA (mtDNA) has been successfully sequenced. DNA was extracted from fin clips using a Nucleospin Tissue kit (Macherey-Nagel, Germany). The COI gene was amplified using the universal M13-tailed primer cocktail for fish DNA barcoding (Ivanova *et al.*, 2007). The 25  $\mu$ l PCR reactions included 2.5  $\mu$ l of PCR buffer (10 $\times$ ), 2.5  $\mu$ l of dNTP (2 mM), 1.25  $\mu$ l of primer cocktail (2  $\mu$ M), 0.2  $\mu$ l of Taq DNA polymerase (5 units per  $\mu$ l), 2.0  $\mu$ l of extracted DNA and 16.75  $\mu$ l of mQ-H<sub>2</sub>O. The PCR profile was 3 min at 94°C, followed by 35 cycles of 45 s at 94°C, 40 s at 51°C, 1 min 30 s at 72°C and ending with a final extension of 10 min at 72°C (Decru *et al.*, 2016). Amplification was visually checked on 1.2% agarose gels, and PCR products were purified using an ExoSAP-IT PCR Clean-up Kit (Affymetrix, Inc.; Thermo Fisher Scientific, Waltham, MA, USA). Standard Sanger Sequencing was executed by the external company Macrogen, where samples were sequenced bidirectionally using an ABI 3730XL capillary sequencer. The DNA sequences were assembled and visually checked in CodonCode Aligner 4.2.7 (CodonCode Corporation; Centerville, MA, USA) and aligned and analysed in MEGA 7.02. Sequences from Genbank from *Genomyrus donnyi* were included as an outgroup. Unfortunately, for *C. cubangoensis*, no samples nor sequences on Genbank were available. A model test was performed and the HKY + G was chosen as the most suitable model under the akaike information criterion. Maximum likelihood (ML) trees with 500 bootstrap replications were produced. The sequences, including the paragenotype of the new species, were deposited in GenBank for future reference (Supporting Information Table S1).

## 2.4 | Abbreviations

AIC, Akaike Information Criterion; a.s.l., above sea level; BEZHU, Biodiversité et Exploitation durable des Zones Humides; COI, cytochrome c oxidase subunit; CTB/BTC, Coopération Technique Belge/Belgische Technische Coöperatie; CU, Cornell University; DEA, Diplôme d'Etudes Approfondies; DRC, Democratic Republic of the

Congo; ISP, Institut Supérieur Pédagogique; KNP, Kundelungu National Park;  $L_H$ , head length;  $L_S$ , standard length;  $L_T$ , total length; mtDNA, mitochondrial DNA; MNHN, Musée National d'Histoire Naturelle, Paris, France; MRAC, Musée Royal de l'Afrique Centrale, Tervuren, Belgium; MWU-test, Mann-Whitney U-test; NHM, Natural History Museum, London, UK; PC, principal component; PCA, principal components analysis; RMCA, Royal Museum for Central Africa, Tervuren, Belgium; SAIAB, South African Institute for Aquatic Biodiversity, Grahamstown, South Africa; UNIKOL, Université de Kolwezi; UNILU, Université de Lubumbashi; UNP, Upemba National Park; ZMB, Zoologisches Museum Berlin, Berlin, Germany; ZSM, Zoologisches Staatssammlung München, München, Germany.

### 3 | RESULTS

#### 3.1 | Motivation for the generic transfer of *H. aelsbroecki* (Pellegrin 1936) to the genus *Cyphomyrus*

*Hippopotamyrus aelsbroecki* (Poll 1945) was originally described as a *Gnathonemus* species based on a single specimen, the holotype, from Lubumbashi, most probably the Lubumbashi River, which is a left bank affluent of the Kafubu River, itself a left bank affluent of the Luapula River. In his original description, Poll (1945) reports that *G. aelsbroecki* belongs to the small group of *Gnathonemus* species with a dorsal fin that is much longer than the anal one and clearly originates in front of the insertion level of the latter. In his osteological and morphological work on the genera *Gnathonemus*, *Marcusenius*, *Hippopotamyrus* and *Cyphomyrus*, Taverne (1971) reassigned *G. aelsbroecki* to the genus *Hippopotamyrus* Pappenheim 1906. In the same work, Taverne (1971) also synonymised the genus *Cyphomyrus* with *Hippopotamyrus*, this based on some osteological evidence only: (a) the shared presence of a well-developed lateral ethmoid; (b) five circumorbital bones with the antorbital and first infraorbital fused; (c) the same shape and arrangement of the bones of the snout and lower jaw; and (d) the presence of five hypural bones in the caudal skeleton. However, as *G. aelsbroecki* was described on a single specimen, the holotype, and no other specimens had been collected since, its attribution to the genus *Hippopotamyrus* must have been based on external morphological evidence only. Later on, the genus *Cyphomyrus* was rehabilitated by Van der Bank and Kramer (1996) based on: (a) external morphological evidence; (b) the waveforms of the EOD; and (c) an allozyme study on *C. discorhynchus*. Subsequently, a mitochondrial DNA sequence analysis using cytochrome b was also performed which demonstrated that the genus *Cyphomyrus*, including its type species *C. psittacus*, is different from the sympatric *Hippopotamyrus ansorgii* species complex (Kramer et al., 2004; Kramer & Swartz, 2010; Van der Bank & Kramer, 1996). However, the generic assignment of this species complex remains problematic and further combined mitochondrial and nuclear molecular evidence revealed that it requires classification into a different genus (see Sullivan et al., 2016: Figure 5).

After morphologically examining the holotype of *H. aelsbroecki* (Figure 1a,b) and considering the diagnostic characters presented by

Poll (1945), Myers (1960) and Kramer and Swartz (2010) for the genus *Cyphomyrus*, *H. aelsbroecki* corresponds well to the diagnosis of this genus. So, certainly the long dorsal fin, with its origin well ahead of that of the anal fin and its posterior end just posterior to that of the anal fin [vs. anterior and posterior end of both dorsal and anal fin, at the same vertical level (as observed in *H. castor*, type species of the genus *Hippopotamyrus*) or the origin of the dorsal fin even a little behind that of the anal fin as in some other species of the genus *Hippopotamyrus*] distinguishes *Cyphomyrus* from *Hippopotamyrus* (Hopkins et al., 2007; Myers, 1960). Additional characters are the rounded or arched predorsal profile and the deep and compact body of *Cyphomyrus* (Kramer & Van der Bank, 2011; Myers, 1960) [vs. a straight or convex predorsal profile but not vaulted with a rather elongated body of moderate depth for the genus *Hippopotamyrus* (Hopkins et al., 2007; Myers, 1960)]. As such, *Hippopotamyrus aelsbroecki* is here transferred to the genus *Cyphomyrus* as it conforms with the diagnostic characters of the genus as provided above following Myers (1960) and Kramer and Van der Bank (2011).

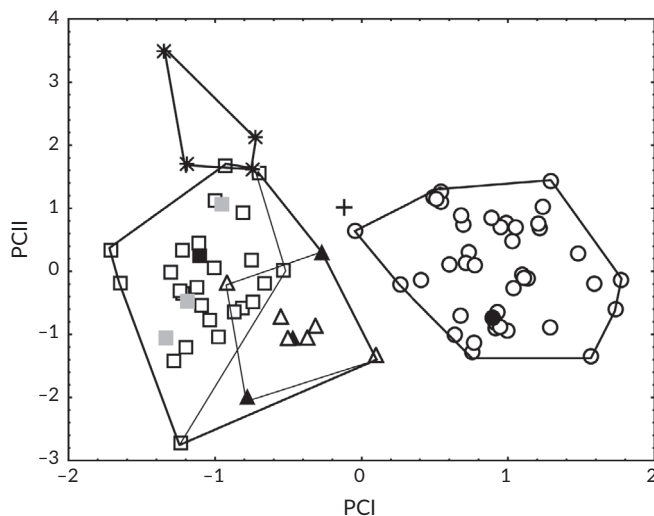
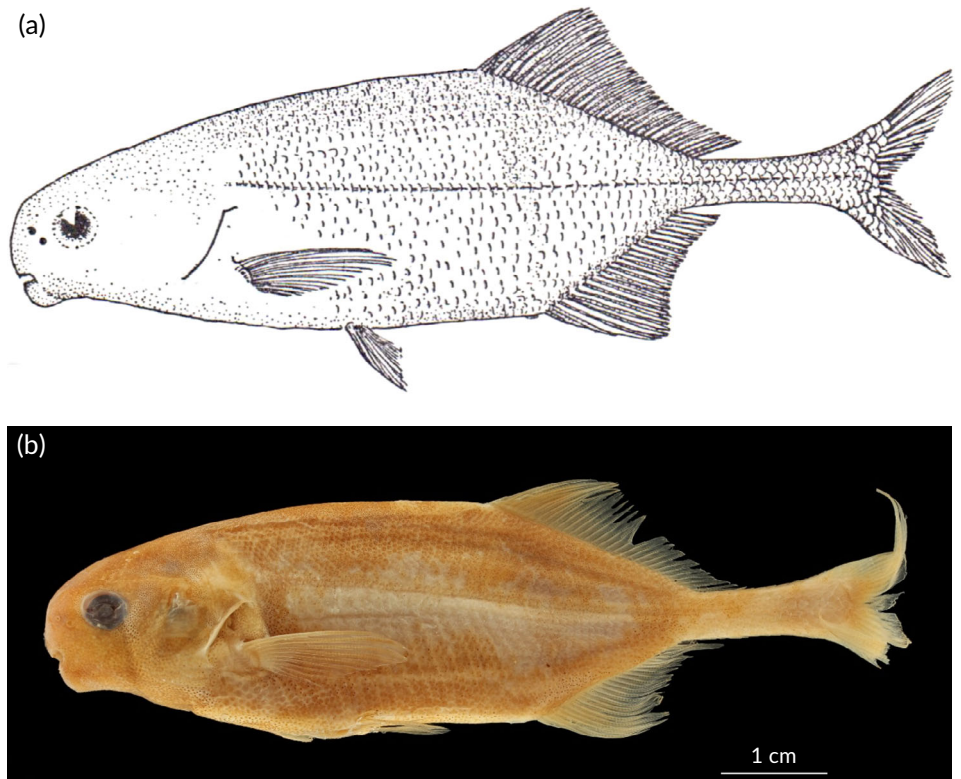
#### 3.2 | Analysis of the meristics

A first PCA was carried out on 10 meristics for all examined specimens ( $n = 90$ ) (Figure 2). The most important loadings on PCI were for the number of circumpenduncular scales, the number of pectoral-fin rays, the number of dorsal-fin rays and the number of scales between the dorsal and anal fins. The highest loadings on PCII were for the number of scales between the pelvic fin and the lateral line and the number of anal-fin rays (Table 1a).

Four groups can be distinguished on this PCA (Figure 2). First, the three groups on the left-hand side and mainly situated on the negative side of PCI contain (a) the lectotype and the four paralectotypes of *C. discorhynchus*, and the specimens of Lake Kariba (Zambezi basin) and the Upper Lualaba (Congo basin) all also attributed to this species, these mainly situated on the negative side of PCII, (b) the three examined syntypes of *C. tanganicanus*, a current junior synonym of *C. discorhynchus*, as well as some additional specimens from the Lake Tanganyika affluents, these also mostly situated on the negative side of PCII, and (c) the four examined syntypes of *C. cubangoensis*, these entirely situated on the positive side of PCII. Second, the fourth group, that is the only one situated on the right-hand side and almost entirely on the positive side of PCI, contains the specimens from the Middle and Lower Lufira here recognized as a new species for science and named *C. lufirae*. In addition, the holotype of *C. aelsbroecki* is located near to the 0 point of PCI and slightly on the positive side of PCII.

Mann-Whitney U (MWU) tests, with sequential Bonferroni correction, were performed on all meristics included in the PCA (Table 1b). Between *C. lufirae* and *C. discorhynchus*, eight out of the 10 meristics were found to be highly significant ( $P \leq 0.001$  after Bonferroni correction). Furthermore, between *C. lufirae* and *C. tanganicanus*, a current junior synonym of *C. discorhynchus*, five out of the 10 meristics were found to be significantly different, three of which were highly significantly different. In addition, between *C. lufirae* and *C. cubangoensis*, four

**FIGURE 1** *Cyphomyrus aelsbroeckii*, MRAC 54990, holotype, female, 71.4 mm  $L_S$ , DRC: Lubumbashi (former Elisabethville): (a) drawing of the holotype (Poll, 1945: Figure 4) and (b) photograph of the preserved holotype



**FIGURE 2** Scatterplot of PCI against PCII for a PCA on 10 meristics for all examined specimens ( $n = 90$ ). *Cyphomyrus aelsbroeckii*: +, holotype; *C. cubangoensis*: \*, syntypes; *C. discorhynchus*: ■, lectotype; □, paralectotypes; □, specimens from the Kamalondo Depression; *C. lufirae*: ●, holotype; ○, other specimens; *C. tanganicus* (currently a junior synonym of *C. discorhynchus*): ▲, syntypes; △, other specimens from some affluents of the Lake Tanganyika basin

meristics were found to be significantly different, of which a single one was highly significantly different.

After the MWU tests, meristic variables whose differences were significantly or highly significantly different were also evaluated using scatterplots to identify those that could be used as good diagnostic characters for species identification. Four meristic characters with

slightly overlapping values separate *C. lufirae* from *C. discorhynchus* (Figure 3a-d), and three characters with slightly overlapping values separate *C. lufirae* from *C. cubangoensis* (Figure 3a-c). In addition, specimens of *C. lufirae* have a higher number of scales between the anterior base of the dorsal fin and the anterior base of the anal fin compared to *C. aelsbroeckii* (Figure 3d).

### 3.3 | Analysis of the measurements

A second PCA was carried out on 28 measurements in percentages ( $n = 90$ ) (Figure 4). The most important loadings on PCI were for the prepelvic length, the prepectoral length, the length of the head, the distance between the pelvic fin and the anal fin, and the depth of the caudal peduncle. The highest loadings on PCII were for the distance between the pectoral and anal fins, the body depth at the dorsal fin insertion and depth of the head (Table 2a).

Two major groups can be distinguished on this PCA (Figure 4). First, a major group situated mainly on the positive side of PCI contains: (a) the lectotype and the four paralectotypes of *C. discorhynchus* and the specimens from Lake Kariba (Zambezi basin) and the Upper Lualaba (Congo basin) all also attributed to this species and all mainly situated on the negative side of PCII; (b) the three studied syntypes of *C. tanganicus*, a current junior synonym of *C. discorhynchus*, and some additional specimens from the Lake Tanganyika basin affluents; (c) the syntypes of *C. cubangoensis*; and (d) the holotype of *C. aelsbroeckii* all situated mainly or entirely on the positive side of PCII. Second, a major group situated on the negative part of the PCI only contains the specimens of the new species for science, *C. lufirae*.

**TABLE 1** (a) PC loadings for the first three PCs of the PCA performed on 10 meristics for all examined specimens ( $n = 90$ )

Variable	(a) PC loadings			(b) MWU tests		
	PCI	PCII	PCIII	<i>C. lufirae</i> vs. <i>C. discorhynchus</i>	<i>C. lufirae</i> vs. <i>C. tanganicanus</i>	<i>C. lufirae</i> vs. <i>C. cubangoensis</i>
Dorsal-fin rays	-0.788139	-0.414011	-0.278887	**	**	NS
Anal-fin rays	-0.638195	-0.574585	-0.378570	**	*	NS
Pectoral-fin rays	-0.863405	0.109295	-0.270942	**	NS	**
Scales on lateral line	-0.650228	-0.394094	0.220513	**	**	NS
Circumpeduncular scales	0.896880	0.051097	-0.012001	**	**	*
Scales between dorsal and anal fins	0.775920	-0.542607	-0.003062	**	NS	*
Scales between dorsal fin and lateral line	0.628621	-0.514933	0.081631	**	NS	*
Scales between pelvic fin and lateral line	0.446454	-0.628891	0.010822	NS	NS	NS
Teeth in upper jaw	-0.634800	-0.027332	0.360443	**	NS	NS
Teeth in lower jaw	-0.497661	-0.215868	0.735743	NS	*	NS

Note (a). *Cyphomyrus aelsbroeckii*: holotype ( $n = 1$ ); *C. cubangoensis*: syntypes ( $n = 4$ ); *C. discorhynchus*: lectotype ( $n = 1$ ), paralectotypes ( $n = 4$ ), and additional specimens ( $n = 25$ ); *C. lufirae*: holotype ( $n = 1$ ), paratypes ( $n = 10$ ) and additional specimens ( $n = 34$ ); *C. tanganicanus* (currently a junior synonym of *C. discorhynchus*): syntypes ( $n = 3$ ) and additional specimens from some affluent rivers of the Lake Tanganyika basin ( $n = 7$ ). Bold values indicate the most important variables. (b) Results of Mann-Whitney U-tests with sequential Bonferroni correction for the 10 meristics. Note (b). NS, not significant; \*significant,  $\alpha = 0.05$ ; \*\*highly significant,  $\alpha = 0.001$ .

MWU tests, with sequential Bonferroni correction, were performed for all measurements included in the PCA (Table 2b). Between *C. lufirae* and *C. discorhynchus*, 12 out of the 29 measurements were found to be significantly different ( $P \leq 0.05$  after Bonferroni correction), 10 of which were highly significantly different ( $P \leq 0.001$ ). Furthermore, between *C. lufirae* and *C. tanganicanus*, a current junior synonym of *C. discorhynchus*, 11 out of the 29 measurements were found to be significant different, seven of which were highly significantly different. Between *C. lufirae* and *C. cubangoensis*, two out of the 29 measurements were found to be significantly different.

After the MWU tests, variables whose differences are significantly or highly significantly different were also evaluated using scatterplots to identify those that could be used as diagnostic characters for species identification. The differentiating characters between *C. lufirae* and *C. cubangoensis* and *C. discorhynchus*, respectively, are the caudal peduncle depth, 6.9–8.4%  $L_S$  (vs. 6.1–6.7% and 5.7–7.0%  $L_S$ , respectively) and the prepelvic length, 41.0–43.8%  $L_S$  (vs. 38.9–39.1% and 37.0–41.0%  $L_S$ , respectively) (Figure 5).

### 3.4 | Molecular data: DNA barcoding

On the ML tree based on COI (mtDNA), the 12 sequences of *C. lufirae* constitute a different clade, from a genetic distance of 1.2% with *C. discorhynchus* (Figure 6).

### 3.5 | *Cyphomyrus lufirae* sp. nov.

Figures 7a,b and 8a, and Table 3.

#### 3.5.1 | Holotype

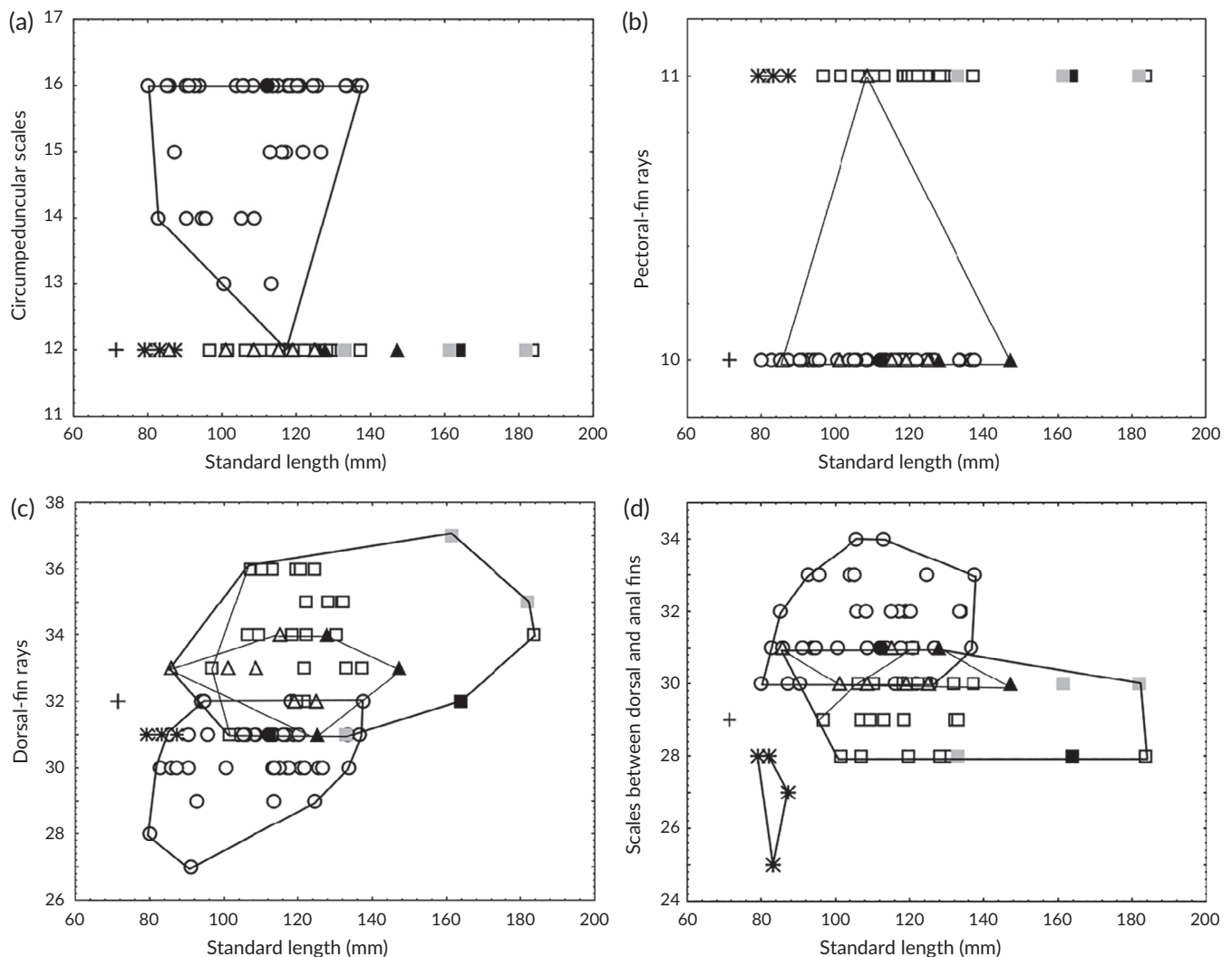
MRAC 2015-005-P-145, female, 112.2 mm  $L_S$ ; DRC: UNP, Lualaba Province, Dikulwe River (Bunkeya-Kyubo), Middle Lufira River, Upper Lualaba (09°57'18.6"S; 026°56'47.1"E); Alt. 888 m above sea level (a.s.l.), Upemba National Park Expedition 2014, 23 October 2014.

#### 3.5.2 | Paratypes

MRAC 2015-005-P-146-148, 115.0–126.6 mm  $L_S$ ; same data as holotype. MRAC 2015-005-P-149-150, 103.8–113.6 mm  $L_S$ ; DRC: UNP, Lualaba Province, Dikulwe River (Kijiba Kikwepe, village Kalwa), Middle Lufira River, Upper Lualaba (09°57'18.6"S; 026°56'47.1"E); Alt. 888 m a.s.l., Upemba National Park Expedition 2014, 25 October 2014. MRAC 2015-005-P-151, 105.8 mm  $L_S$ ; same data as holotype; 22 October 2014. MRAC 2015-005-P-155, 108.6 mm  $L_S$ ; same data as holotype; 21 October 2014. AMNH 275001 (formerly MRAC 2015-005-P-152), 92.6 mm  $L_S$ ; same data as MRAC 2015-005-P-151. BMNH 2019.9.23.1 (formerly MRAC 2015-005-P-153), 94.5 mm  $L_S$ ; same data as MRAC 2015-005-P-151. ZSM 47511 (formerly MRAC 2015-005-P-154), 90.3 mm  $L_S$ ; same data as MRAC 2015-005-P-151.

#### 3.5.3 | Additional non-type material examined

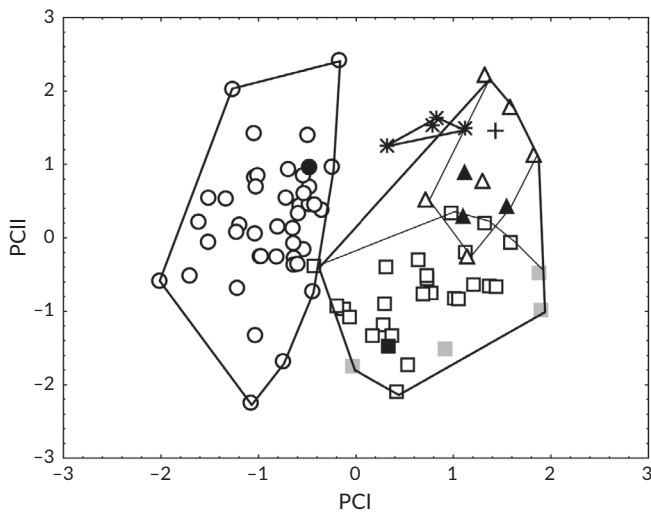
MRAC 2015-005-P-0196-0197, 93.8–103.0 mm  $L_S$ ; same locality as holotype; Coll. C. Mukweze, B. Katemo & J. S. Kiwele, 22 October 2014. MRAC 2015-006-P-0613, 116.1 mm  $L_S$ ; DRC: KNP, Haut-Katanga Province, Kafila River (village Kienge), Middle Lufira River, right affluent of the



**FIGURE 3** Scatterplots of the number of (a) circumpeduncular scales, (b) pectoral-fin rays, (c) dorsal-fin rays and (d) scales between dorsal and anal fins against standard length (in mm) ( $n = 90$ ). *Cyphomyrus aelsbroeckii*: +, holotype; *C. cubangoensis*: \*, syntypes; *C. discorhynchus*: ■, lectotype; ▀, paralectotypes; □, specimens of the Kamalondo Depression; *C. lufirae*: ●, holotype; ○, other specimens; *C. tanganicanus* (currently a junior synonym of *C. discorhynchus*): ▲, syntypes; △, other specimens from some affluents of the Tanganyika basin

Upper Lualaba ( $10^{\circ}33'2''S$ ;  $27^{\circ}29'2''E$ ); Alt. 898 m a.s.l.; Coll. E. Abwe, G. Kapepula & C. Kalombo, 20 August 2014. MRAC 2015-006-P-0715-0176, 113.6–120.2 mm  $L_S$ ; same data as MRAC 2015-006-P-0613. MRAC 2015-006-P-0717, 118.1 mm  $L_S$ ; DRC: KNP, Haut-Katanga Province, Lufira River (village Kapiri), Middle Lufira River, right affluent of the Upper-Lualaba ( $9^{\circ}41'47''S$ ;  $27^{\circ}13'28''E$ ); 872 m a.s.l.; Coll. E. Abwe, G. Kapepula & C. Kalombo, 19 October 2014. MRAC 2016-002-P-0240-0244, 85.7–137.5 mm  $L_S$ ; DRC: KNP, Haut-Katanga Province, Kafila River (Kivuko, Mwadingusha-Kienge road), Middle Lufira River, right affluent of the Upper Lualaba ( $10^{\circ}35'45''S$ ;  $27^{\circ}31'26''E$ ); 875 m a.s.l.; Coll. E. Abwe, G. Kapepula & C. Kalombo, 20 October 2015. MRAC 2016-002-P-0316, 133.3 mm  $L_S$ ; DRC: KNP, Haut-Katanga Province, Luvua River (road bridge Sampwe-Mukana), Middle Lufira River, right affluent of the Upper Lualaba ( $9^{\circ}19'22''S$ ;  $27^{\circ}22'17''E$ ); 911 m a.s.l.; Coll. E. Abwe, G. Kapepula & C. Kalombo, 16 August 2015. MRAC 2015-005-P-0193-0195, 100.4–124.5 mm  $L_S$ ; DRC: UNP, Haut-

Katanga Province, Lufira River (approximate downstream of Kyubo Falls), Middle Lufira River, right affluent of the Upper Lualaba ( $9^{\circ}31'3''S$ ;  $27^{\circ}2'10''E$ ); 835 m a.s.l.; Coll. C. Mukweze, B. Katemo & S. Kiwele, 18 October 2014. MRAC 2016-025-P-0237, 136.5 mm  $L_S$ ; same locality as MRAC 2015-05-P-0193-0195; Coll. E. Vreven, B. Katemo, M. Kasongo, J. Mulagizi & S. Kiwele, 14 August 2016. MRAC 2015-005-P-0190-0192, 72.9–85.8 mm  $L_S$ ; DRC: UNP, Haut-Katanga Province, Luvilombo River (downstream tributary left of Lower Lufira basin after Luvilombo's small Falls), Lower Lufira River, right affluent of the Upper Lualaba ( $9^{\circ}31'6''S$ ;  $27^{\circ}2'7''E$ ); 858 m a.s.l.; Coll. C. Mukweze, B. Katemo & S. Kiwele, 18 October 2014. MRAC 2012-031-P-2165-2176, 85.1–121.7 mm  $L_S$ ; DRC: KNP, Haut-Katanga Province, Lufira River (upstream of Kyubo Falls), Middle Lufira River, right affluent of the Upper Lualaba ( $9^{\circ}31'0''S$ ;  $27^{\circ}2'51''E$ ); 871 m a.s.l.; Coll. E. Vreven, A. Chocha, M. Katemo, E. Abwe & M. Kasongo, 16 September 2012. MRAC 2016-038-P-0017-0023, 113.2–125.5 mm  $L_S$ ; DRC:



**FIGURE 4** Scatterplot of PCI against PCII for a PCA on measurements (in %) for all examined specimens ( $n = 90$ ).

*Cyphomyrus aelsbroeckii*: +, holotype; *C. cubangoensis*: \*, syntypes; *C. discorhynchus*: ■, lectotype; ■, paralectotypes of Lower Zambezi basin; □, specimens of Kamalondo Depression; *C. lufirae*: ●, holotype; ○, other specimens; *C. tanganicus* (currently a junior synonym of *C. discorhynchus*): ▲, syntypes; △, other specimens from some affluents of the Tanganyika basin

KNP, Haut-Katanga Province, Kijiba Mujingi, Kambokoto and Lubumba-shi Lujji River (Nkumbula village), Middle Lufira River, right affluent of the Upper Lualaba ( $9^{\circ}21'49''S$ ;  $27^{\circ}27'44''E$ ); 939 m a.s.l.; C. Mukweze, E. Abwe, P. Kiwele, L. Ngoy & J. Mulagizi, 23 October 2016. MRAC 2015-006-P-0610-0612, 80.0–91.0 mm  $L_S$ ; DRC: KNP, Haut-Katanga Province, Lake Mpungwe (Coopelu village near Kinyonge River), Middle Lufira River, right affluent of the Upper Lualaba ( $10^{\circ}0'7''S$ ;  $27^{\circ}15'32''E$ ); 897 m a.s.l.; Coll. E. Abwe, G. Kapepula & C. Kalombo, 25 October 2014.

### 3.5.4 | Diagnosis

*Cyphomyrus lufirae* (Figure 8a) is distinguished from all its congeners, that is, *C. aelsbroeckii* (Figure 1a,b), *C. cubangoensis* (Figure 8b), *C. discorhynchus* (Figure 8c,d), *C. macrops*, *C. psittacus* and *C. wilverthi*, by a larger caudal peduncle depth, 6.8–8.4%  $L_S$  (vs. smaller, 5.3%, 6.1–6.7%, 5.7–7.0%, 5.2%, 5.8% and 6.2%  $L_S$ , respectively), and a higher number of circumpeduncular scales, 14–16, rarely 12–13 vs. exclusively 12 in all congeners except for *C. discorhynchus*, which rarely also possesses 13 circumpeduncular scales.

In addition, *C. lufirae* differs from *C. macrops*, *C. psittacus* and *C. wilverthi* by a lower number of dorsal fin rays, 27–32 (vs. higher, 36 (37), 34 (33–41) and 38 (38–40), respectively) and from *C. aelsbroeckii*, *C. cubangoensis* and *C. discorhynchus* by a longer prepelvic distance, 41.0–43.8%  $L_S$  (vs. shorter, 39.7%, 38.9–39.1%, and 37.0–41.0%  $L_S$ , respectively).

### 3.5.5 | Description

Based on the holotype, 10 paratypes and 34 additional specimens. Proportional measurements and meristics are given in Table 3 and general appearance is shown in Figure 8. The maximum recorded size of this species was 137.5 mm  $L_S$ . Deep body, 2.8–3.5 times in  $L_S$ , laterally compressed. Predorsal profile convex. Head broadly rounded, 3.4–3.9 times in  $L_S$ . Snout rounded and projecting beyond mouth, 4.1–5.2 times in  $L_H$ . Mouth small and inferior. Chin with a short bulbous protuberance, nostrils closer to eye than mouth. Interorbital space 3.0–4.2 times in  $L_H$ . Dorsal and anal fins obliquely orientated. Dorsal fin length equal or slightly longer than head, its origin situated anterior to anal-fin origin, and its base longer than that of the anal fin. Distance between pelvic and anal fins relatively equidistant to pectoral-fin length. Distal end of pectoral fin pointed, shorter than head length. Caudal peduncle 2.4–3.2 times as long as deep.

### 3.5.6 | Colouration in life

Overall body coloration of *C. lufirae* dull silver, tinged with black and brown and yellowish overtone especially on head. Yellowish coloration more intense in specimens from downstream Kyubo Falls and from Luvilombo River. Fins greyish to black yellowish at their base (Figure 8a). The silver coloration in particular is sometimes less intense or translucent for pelvic and caudal fins. With an oblique black band from anterior base of dorsal-fin up to third or fourth scale row below the lateral line. The oblique black band is less conspicuous in darker coloured specimens, but is more discernible in the yellowish coloured specimens of Lower Lufira, and Luvilombo River.

### 3.5.7 | Colouration in alcohol

Specimens from the Middle Lufira chocolate to blackish whereas those from Lower Lufira yellowish or brown. Oblique black band often becoming more distinguishable than in life. Fins greyish to black or translucent.

### 3.5.8 | Distribution, habitat diversity and ecology

*Cyphomyrus lufirae* is known from the Middle Lufira (Figures 9a,b and 10) and from the Lower Lufira, from the foot of the Kyubo Falls (Figure 9c) and from its nearby left bank affluent the Lower Luvilombo River (Figure 9d). The species is currently thus considered to be endemic to the Middle and Lower Lufira basin.

The species was recorded in river sections with moderate current at all localities on the Lower and Middle Lufira. The depth of the water was variable, about 50 cm in the Luvilombo River, about 5 m in the



**TABLE 2** (a) PC loadings for the first two PCs of the PCA performed on 29 measurements for all examined specimens ( $n = 90$ ), (b) Results of Mann-Whitney U-tests with sequential Bonferroni correction for the 29 measurements

Variables transformed in percentages	(a) PC loadings		(b) MWU tests		
	PCI	PCII	<i>C. lufirae</i> vs. <i>C. discorhynchus</i>	<i>C. lufirae</i> vs. <i>C. tanganicus</i>	<i>C. lufirae</i> vs. <i>C. cubangoensis</i>
Standard length	-	-	NS	NS	NS
Body depth	-0.63247	-0.56270	NS	**	NS
Body depth at the insertion of the dorsal fin	-0.44469	-0.69368	NS	*	NS
Caudal peduncle depth	-0.70181	0.16343	**	**	NS
Caudal peduncle length	-0.20532	0.56598	*	NS	NS
Predorsal distance	-0.149171	-0.47962	NS	NS	NS
Post-dorsal distance	-0.08316	-0.03777	NS	NS	NS
Preanal distance	-0.54930	-0.53307	NS	**	NS
Prepelvic length	-0.91935	0.03779	**	**	*
Prepectoral length	-0.84823	0.28055	**	**	NS
Dorsal-fin length	0.27961	-0.59114	**	NS	NS
Anal-fin length	0.51849	-0.17853	*	NS	NS
Pelvic-fin length	-0.14617	-0.14964	NS	NS	NS
Pectoral-fin length	-0.05223	-0.06372	NS	NS	NS
Distance between pectoral and pelvic fin	-0.73046	-0.39380	**	**	*
Distance between pelvic and anal fin	0.46313	-0.68396	**	NS	NS
Distance between pectoral and anal fin	0.10584	-0.72570	NS	NS	NS
Head length	-0.74601	0.23323	**	*	NS
Head depth	-0.23301	-0.64009	NS	NS	NS
Head width	0.00807	-0.39557	NS	NS	NS
Interorbital width	-0.40923	0.12271	**	NS	NS
Eye diameter	0.07407	-0.15632	NS	NS	NS
Post-orbital length	0.32712	0.00471	NS	NS	NS
Snout length 1 (SNL)	-0.21003	-0.21622	NS	NS	NS
Length of snout 2 (LSo)	-0.14582	-0.16867	NS	NS	NS
Length of snout 3 (LSc)	-0.27010	-0.11845	NS	NS	NS
Distance between nostrils	0.08866	0.33204	NS	*	NS
Distance between nostril and eye	-0.61675	-0.01456	**	**	NS
Length of the gill opening	0.59918	-0.40354	**	*	NS

Note (a). *C. aelsbroeckii*: (holotype) ( $n = 1$ ); *C. cubangoensis*: syntypes ( $n = 4$ ); *C. discorhynchus*: lectotype ( $n = 1$ ), paralectotypes ( $n = 4$ ), and additional specimens ( $n = 25$ ); *C. lufirae*: holotype ( $n = 1$ ), paratypes ( $n = 10$ ) and additional specimens ( $n = 34$ ); *C. tanganicus* (currently a junior synonym of *C. discorhynchus*): syntypes ( $n = 3$ ), and additional specimens from some affluent rivers of the Lake Tanganyika basin ( $n = 7$ ). Bold values indicate the most important variables. Note (b). NS, not significant; \*, significant,  $\alpha = 0.05$ ; \*\*, highly significant,  $\alpha = 0.001$ .

pool on the Dikulwe River, and about 10 m just downstream of the Kyubo Falls on the Lower Lufira River.

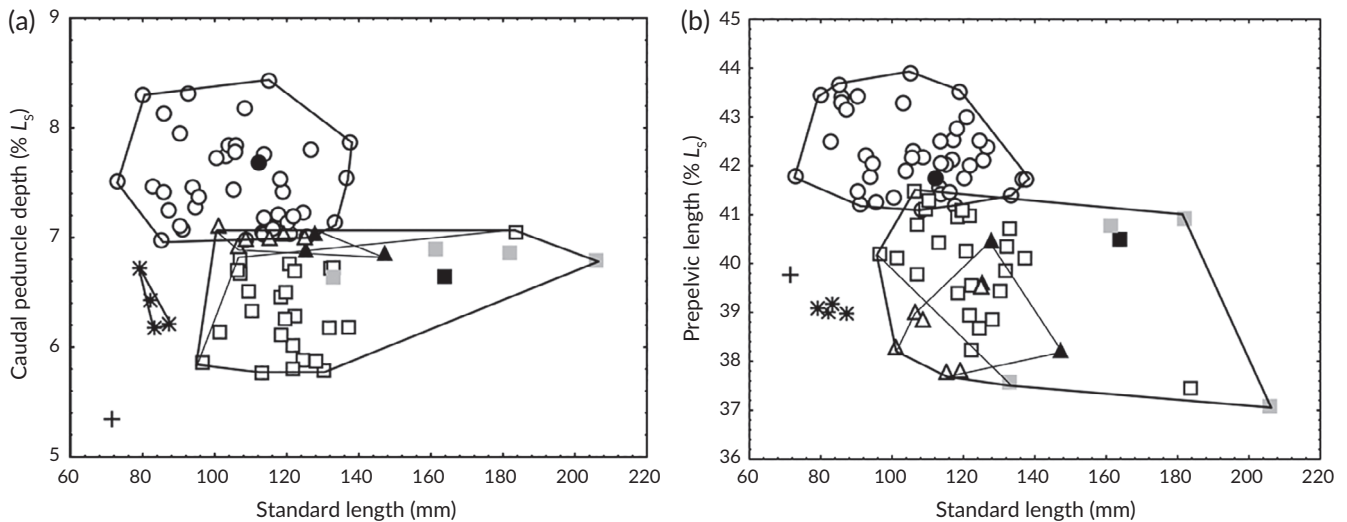
The following physico-chemical parameters of the water were recorded in the Lower and Middle Lufira on 19–23 October 2014 and 11–18 August 2016 during the morning, between 8 and 10 a.m.: temperature 23.6–26.6°C; pH 7.9–8.3 except for the type locality where it is acidic, 5.3–6.2; dissolved oxygen 5.82–7.19 mg l<sup>-1</sup> (73.1–94.1%) and conductivity 8.0–468.4  $\mu\text{S cm}^{-1}$  but reaching more than double the type locality or 778.9 and 913.2  $\mu\text{S cm}^{-1}$ .

### 3.5.9 | Etymology

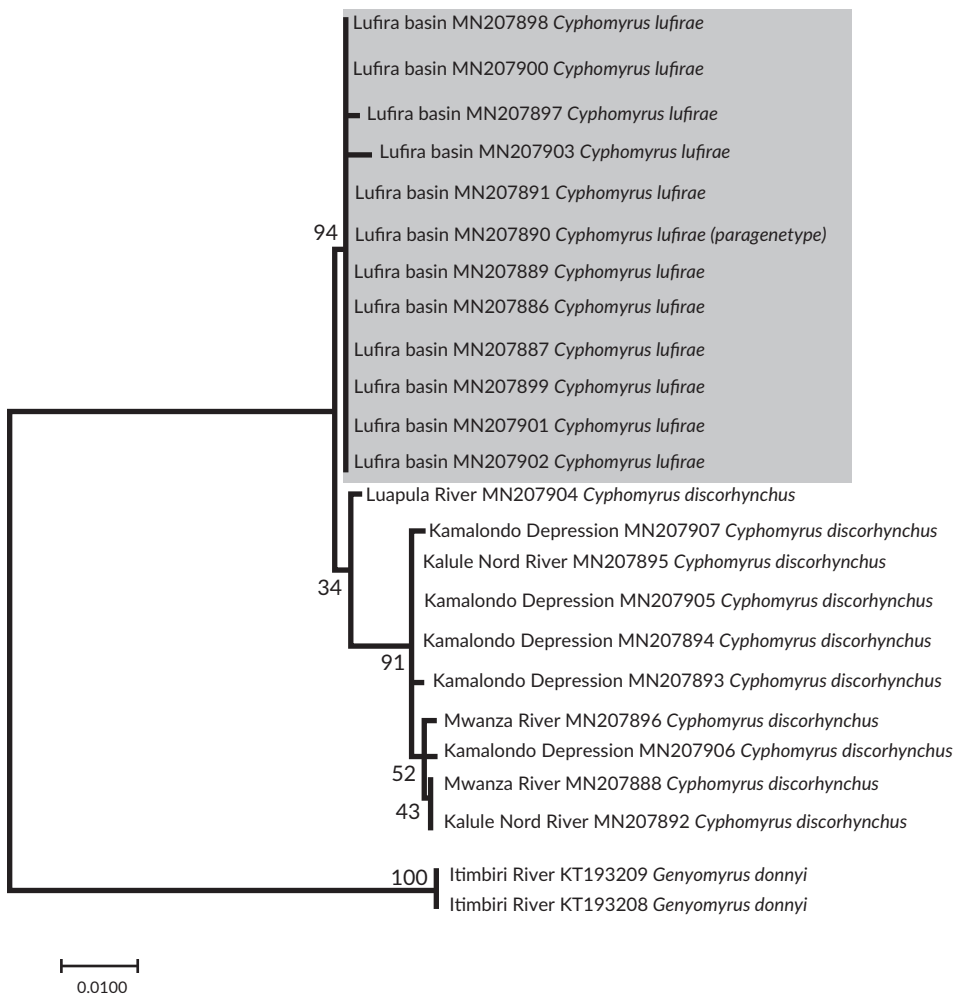
The specific name, *lufirae*, is a Latin adjective referring to the Lufira River to which the new species seems endemic.

### 3.5.10 | Local knowledge

*Cyphomyrus lufirae* is called 'sengwa' in Sanga (a Bantu language), which refers to the general morphology of the mormyrids of this

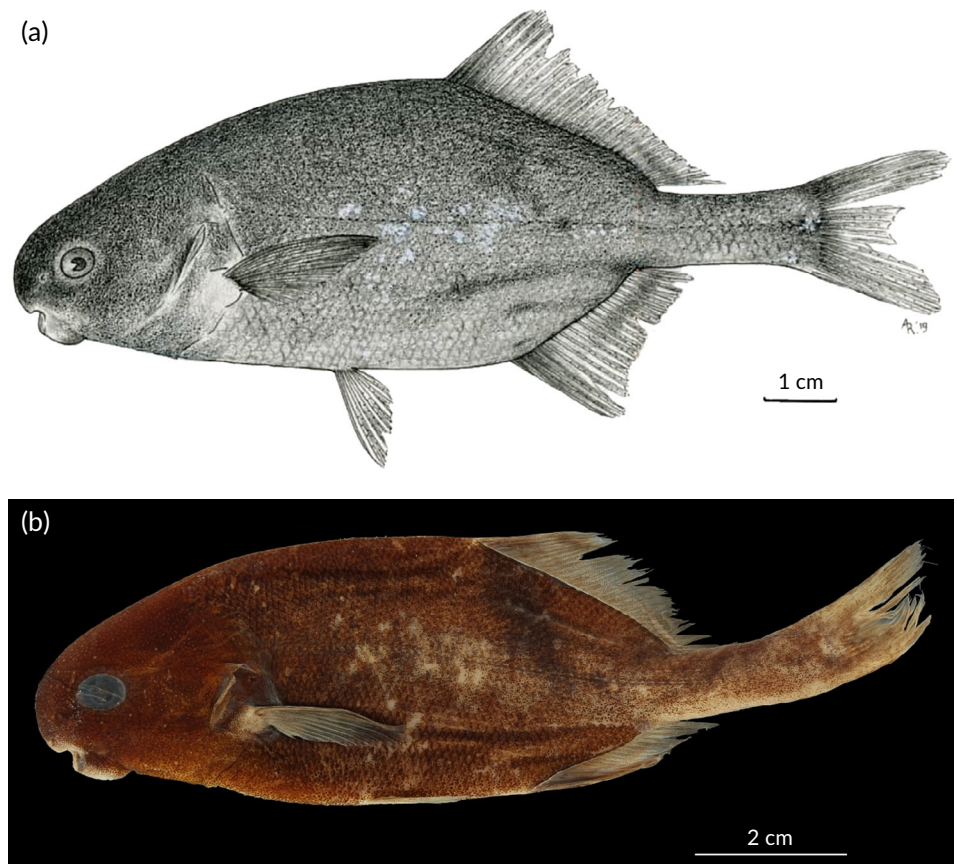


**FIGURE 5** Scatterplots of (a) caudal peduncle depth (%  $L_s$ ) and (b) prepelvic length (%  $L_s$ ) against standard length (in mm) ( $n = 90$ ). *Cyphomyrus aelsbroecki*: +, holotype; *C. cubangoensis*: \*, syntypes; *C. discorhynchus*: ■, lectotype; □, paralectotypes of the Lower Zambezi basin; □, specimens from the Kamalondo Depression; *C. lufirae*: ●, holotype; ○, other specimens; *C. tanganicanus* (currently a junior synonym of *C. discorhynchus*): ▲, syntypes; △, other specimens from some affluents of the Tanganyika basin



**FIGURE 6** Maximum likelihood tree based on the mitochondrial cytochrome c oxidase subunit I (COI) sequences. See text for details on the tree reconstruction method and Supporting Information Table S1 for specimen voucher data and Genbank accession numbers. Statistical node support (500 bootstrap replications) is visualized at each node. The clade of the new species *C. lufirae* is highlighted in grey. The scale bar refers to the branch lengths, measured in the number of substitutions per site

**FIGURE 7** *Cyphomyrus lufirae*, holotype, MRAC 2015-05-P-145, female, 112.2 mm  $L_s$ , DRC: Dikulwe River (bridge Bunkeya-Kyubo), Middle Lufira River: (a) drawing of lateral view and (b) photograph of the preserved specimen

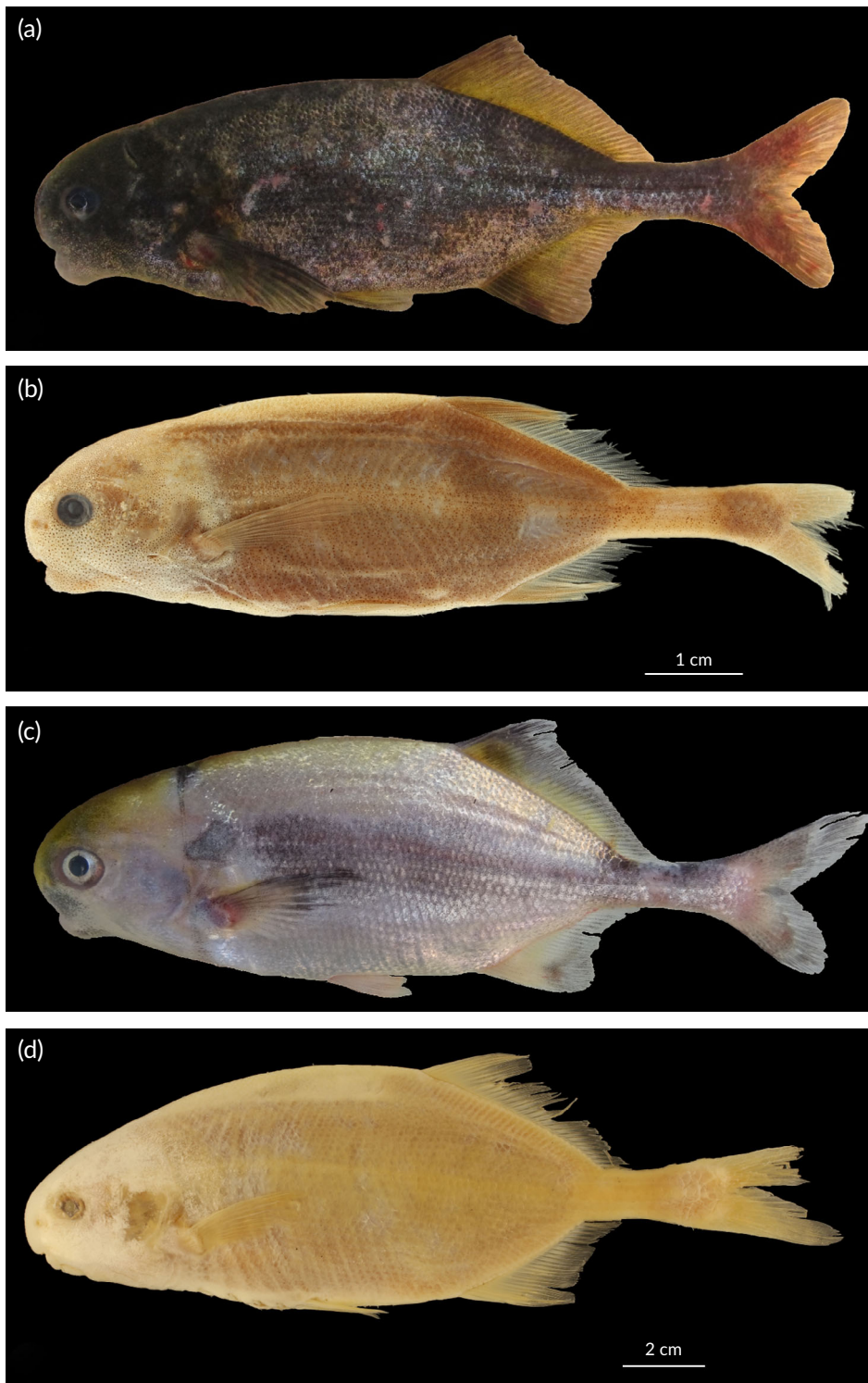


genus as opposed to those from the genus *Hippopotamyrus* and occurring in the same river, which are called 'mbubu' in the same language. This species is highly appreciated by the local inhabitants due to the high fat content of its meat. They prefer to eat it smoked.

#### 4 | DISCUSSION

Within the Lufira basin, a new *Cyphomyrus* species, here named *C. lufirae*, has been discovered. Among all currently known congeners, *C. lufirae* is morphologically most similar to *C. cubangoensis* (see Figure 8b) and *C. discorhynchus* (see Figure 8c,d). However, it differs from both by a deeper caudal peduncle (Figure 5a) and a larger prepelvic distance (Figure 5b). Further, *C. lufirae* is the only species of *Cyphomyrus* known with generally 14–16 circumpeduncular scales, very rarely only 12–13, one and two individual(s) respectively [vs. 12 for all other known *Cyphomyrus* species, although rarely 13 in some specimens of *C. discorhynchus* (Kramer & Van der Bank, 2011)]. Finally, *C. lufirae* usually also has fewer scales on the lateral line, 60–66 [vs. 63–73 for *C. discorhynchus*, with 63–73 scales for specimens of the Upper Lualaba, 67–72 for those of Lake Kariba, 66–70 for those of the Lower Zambezi and 66–70 for those of the Tanganyika basin (*C. tanganicus*: at present a junior synonym of *C. discorhynchus*)]. While *C. cubangoensis* is not known from the Congo basin and only reported from the Okavango and Upper Zambezi basins (Skelton, 2001; Skelton, 2019), *C. discorhynchus* is considered

to have a wide geographical distribution covering the Zambezi and part of the Congo basin *sensu lato* (Skelton, 2001; Scott *et al.*, 2006). Also within the Congo basin, *C. discorhynchus* has a wide distribution range as it has been reported from the Lake Tanganyika basin (Worthington & Ricardo, 1936) up to the Upper Lualaba, that is, the Kamalondo Depression and the Lower Lufira, as well as the Upper Kasai, at Dilolo ( $\pm 10^{\circ} 41' S$ ;  $22^{\circ} 20' E$ ) (Poll, 1976). This widespread distribution is partially the result of the synonymisation of *C. tanganicus*, originally described from Lake Tanganyika (Boulenger, 1906), with *C. discorhynchus* by Boulenger (1909) in his 'Catalog of the Fresh-water fishes of Africa'. Unfortunately he did not provide any justification for this decision. However, examination of the three syntypes of *C. tanganicus* and seven additional specimens from some Lake Tanganyika tributaries revealed meristic (Figure 2) and morphometric (Figure 4) differences with *C. discorhynchus*. The separation of *C. discorhynchus* and *C. tanganicus* on the PCA scatterplot for the meristic data is mainly attributed to differences in the number of pectoral fin rays, as specimens of the former species collected from the Zambezi and Upper Lualaba always had 11 rays, whereas specimens of the latter nominal species collected from the Tanganyika basin always had 10 rays (with the exception of one specimen that had 11). These specimens also showed some marginal differences in body depth and preanal distance (see Figure 11a,b). These preliminary observations could either be interpreted as representing intraspecific variation within *C. discorhynchus*, or an indication that *C. tanganicus* could be a valid species. We have, however, refrained



**FIGURE 8** Photographs of: (a) life specimen of *C. lufirae*, MRAC 2015-006-P-0613, female, 116.1 mm  $L_S$ , DRC: Kafila River (village Kienge), Middle Lufira River, right affluent of the Upper-Lualaba. Photo: Expedition KNP 2015; (b) preserved specimen of *C. cubangoensis* (syntype), MRAC 138760 (ex. MNHN 1936-65), 83.2 mm  $L_S$ ; Angola: Cubango (Okavango) basin; (c) life specimen of *C. discorhynchus*, MRAC 2016-03-P-0148, male, mm  $L_S$ , DRC: Haut Lomami Province: UNP: Lake Lukanga, Kamalondo Depression. Photo: Expedition UNP 2015; and (d) preserved specimen of *C. discorhynchus* (lectotype), ZMB 3674, female, 163.7 mm  $L_S$ , Lower Zambezi

from making any taxonomic decisions for *C. discorhynchus* and its junior synonym, *C. tanganicus*, pending further examination of a more representative sample size as well as generation of additional data including genetics and/or EODs.

The low genetic divergence in COI sequences of *C. lufirae* and the other congeners considered in the present study is consistent with patterns recorded for other morphologically divergent mormyrid species. For example, Kramer *et al.* (2004) recorded mtDNA cyt b sequence

divergence values of 0.6–1.7% between *H. szaboi* and *H. ansorgii*, Kramer and Wink (2013) reported divergences of 0.4–1.6% between *Marcusenius altisambesi* and *M. multiquamatus*, while Kramer *et al.* (2013) reported a divergence value of 1.2% between *Pollimyrus marianne* and *P. cuandoensis*. More recently, Sullivan *et al.* (2016) presented some species pairs within the genera *Campylomormyrus* Bleeker, 1974, *Marcusenius* Gill, 1862, *Petrocephalus* Marcusen, 1854, and *Cyphomyrus*, which had COI sequence divergences less than 1%.

**TABLE 3** Measurements and counts for *C. aelsbroeckii*, *C. cubangoensis*, *C. discorhynchus* (lectotype + paralectotype and other specimens), *C. tanganicanus* (synonym of *C. discorhynchus*) and *C. lufirae*

	<i>C. aelsbroeckii</i>			<i>C. cubangoensis</i>			<i>C. discorhynchus</i>			<i>C. tanganicanus</i> (synonym of <i>C. discorhynchus</i> )			<i>C. lufirae</i>		
	h	s (n = 4)		l	pl (n = 4)		All specimens (n = 25)		s (n = 3)		All specimens (n = 10)		All specimens (n = 45)		
		Mean ± SD	Range		Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range	
Standard length (mm)	71.4	82.9 ± 0.33	79.1–87.2	163.7	170.4 ± 30.9	132.8–205.8	122.3	96.5–183.6	133.3 ± 12.0	125.2–147.1	116.1 ± 16.8	85.7–147.1	112.2	107.7 ± 16.2	72.9–137.5
<b>Percentage of standard length</b>															
Body depth	26.3	27.7 ± 1.8	25.9–30.2	33.2	29.9 ± 2.2	28.1–33.0	31.3 ± 1.5	28.7–33.7	27.0 ± 0.9	26.8–28.1	26.9 ± 1.5	24.6–29.6	32.5	31.7 ± 1.9	28.4–36.9
Body depth at the insertion of the dorsal fin	26.5	27.6 ± 1.2	26.9–29.5	32.5	31.2 ± 2.1	29.3–34.2	31.2 ± 1.6	28.8–35.0	29.6 ± 1.0	28.5–30.4	28.5 ± 1.5	25.3–30.4	31.5	31.0 ± 1.5	28.3–34.8
Caudal peduncle depth	5.3	6.3 ± 0.2	6.1–6.7	6.6	6.8 ± 0.1	6.6–6.9	6.3 ± 0.3	5.7–7.0	6.9 ± 0.0	6.8–7.0	6.9 ± 0.2	6.3–7.1	7.6	7.4 ± 0.4	6.9–8.4
Caudal peduncle length	21.4	23.1 ± 0.7	22.3–24.2	20.2	20.8 ± 0.4	20.5–21.4	20.8 ± 0.9	18.7–22.3	22.1 ± 0.9	21.1–23.0	21.8 ± 0.5	21.1–23.0	21.9	21.8 ± 1.0	19.8–24.0
Predorsal distance	57.1	57.9 ± 0.8	56.7–58.6	60.6	58.8 ± 1.2	58.0–60.7	58.5 ± 1.1	56.9–61.6	59.0 ± 1.3	57.9–60.5	57.7 ± 1.5	55.3–60.5	57.9	58.1 ± 1.1	55.6–60.5
Post-dorsal distance	46.1	46.8 ± 1.1	45.6–48.0	45.2	47.1 ± 0.6	46.4–47.9	47.6 ± 1.3	44.4–50.3	47.0 ± 1.4	45.3–48.2	47.8 ± 1.5	45.3–50.5	47.8	47.9 ± 1.1	44.6–50.5
Prenal distance	62.1	61.3 ± 0.4	60.8–61.7	62.8	63.0 ± 1.5	61.7–65.1	63.0 ± 1.0	61.2–64.7	60.9 ± 0.2	60.6–61.0	60.8 ± 1.1	58.8–62.7	63.9	63.3 ± 1.2	60.7–66.1
Prepelvic length	39.7	39.0 ± 0.0	38.9–39.1	40.5	39.0 ± 2.0	37.0–40.9	40.0 ± 1.0	37.4–41.4	39.4 ± 1.1	38.2–40.4	39.2 ± 1.4	37.7–42.5	41.7	42.1 ± 0.8	40.2–43.9
Prepectoral length	23.9	23.7 ± 0.4	23.2–24.3	22.9	22.1 ± 0.6	21.5–22.9	23.2 ± 0.6	22.3–24.6	22.8 ± 1.3	21.5–24.1	22.9 ± 0.8	21.5–24.1	24.6	24.9 ± 0.8	22.9–27.2
Dorsal-fin length	27.2	26.7 ± 0.7	26.1–27.7	29.4	30.6 ± 1.0	29.3–31.6	29.9 ± 1.5	27.1–33.3	27.7 ± 0.7	27.2–28.5	28.4 ± 1.2	27.1–30.2	29.3	28.3 ± 1.0	24.8–31.1
Anal-fin length	19.9	18.7 ± 0.9	17.9–20.0	20.7	20.5 ± 0.4	20.2–21.1	19.6 ± 1.0	17.8–22.6	19.7 ± 0.6	19.1–20.3	20.0 ± 1.3	18.5–22.3	19.7	18.9 ± 1.0	17.1–21.3
Pelvic-fin length	12.1	13.1 ± 0.3	12.8–13.5	12.5	12.7 ± 0.3	12.3–12.9	13.0 ± 0.6	12.2–14.4	12.6 ± 0.6	12.0–13.3	13.0 ± 0.6	12.0–14.0	12.4	12.9 ± 0.6	11.1–14.2
Pectoral-fin length	21.3	22.4 ± 0.6	21.5–22.9	20.9	21.0 ± 1.4	19.4–22.4	21.5 ± 1.1	19.5–24.1	21.4 ± 0.4	21.2–21.9	21.5 ± 0.8	20.3–22.9	21.2	21.2 ± 1.1	19.1–23.2
Distance between pectoral and pelvic fin	16.0	16.1 ± 0.5	14.5–18.2	18.6	18.6 ± 0.8	17.4–19.3	17.9 ± 0.7	16.6–19.5	17.1 ± 0.4	16.7–17.6	17.2 ± 0.7	15.8–18.4	18.4	19.1 ± 0.7	17.2–20.5
Distance between Pelvic and anal fin	22.5	21.8 ± 0.5	21.1–22.2	20.9	23.9 ± 0.6	23.2–24.7	23.2 ± 0.9	21.9–25.1	22.7 ± 0.7	22.1–23.6	21.8 ± 1.1	20.4–23.6	19.9	21.5 ± 1.1	19.0–23.5
Distance between pectoral and anal fin	37.6	37.4 ± 1.0	36.1–38.5	41.0	41.5 ± 1.2	40.8–43.5	39.7 ± 1.0	37.6–41.5	39.6 ± 0.7	38.8–40.4	38.6 ± 1.4	35.5–40.9	36.8	38.9 ± 1.6	35.3–42.4
Head length	25.8	26.2 ± 0.6	25.4–26.9	24.5	23.6 ± 0.9	22.6–24.7	25.9 ± 0.8	24.8–27.9	25.1 ± 1.0	23.9–25.7	25.4 ± 1.0	23.9–27.6	26.5	27.0 ± 0.9	25.3–28.9
<b>Percentage of head length</b>															
Head depth	83.0	87.3 ± 2.7	84.9–91.1	102.7	96.9 ± 4.4	91.3–100.7	96.2 ± 5.2	84.8–103.8	90.0 ± 1.8	87.9–91.3	89.1 ± 4.7	81.5–97.0	99.2	94.1 ± 6.1	84.6–114.8
Head width	44.3	46.0 ± 0.9	44.7–46.8	48.2	44.2 ± 1.7	42.3–46.2	47.2 ± 2.0	47.2–50.9	47.0 ± 0.1	46.8–47.2	46.7 ± 1.6	43.1–48.7	44.2	46.0 ± 3.0	38.8–53.2
Interorbital width	28.5	25.3 ± 0.8	24.0–25.9	26.9	26.2 ± 1.3	25.0–27.7	25.6 ± 1.2	22.1–28.0	26.8 ± 0.9	26.0–27.8	26.8 ± 1.1	24.7–29.0	26.9	28.3 ± 2.3	23.2–32.6
Eye diameter	24.1	22.5 ± 0.3	22.3–22.9	22.5	22.2 ± 1.5	20.8–24.3	23.6 ± 1.2	21.6–25.3	24.2 ± 1.0	22.9–24.8	24.0 ± 1.0	22.4–25.5	23.2	23.1 ± 1.4	20.1–26.5

(Continues)

TABLE 3 (Continued)

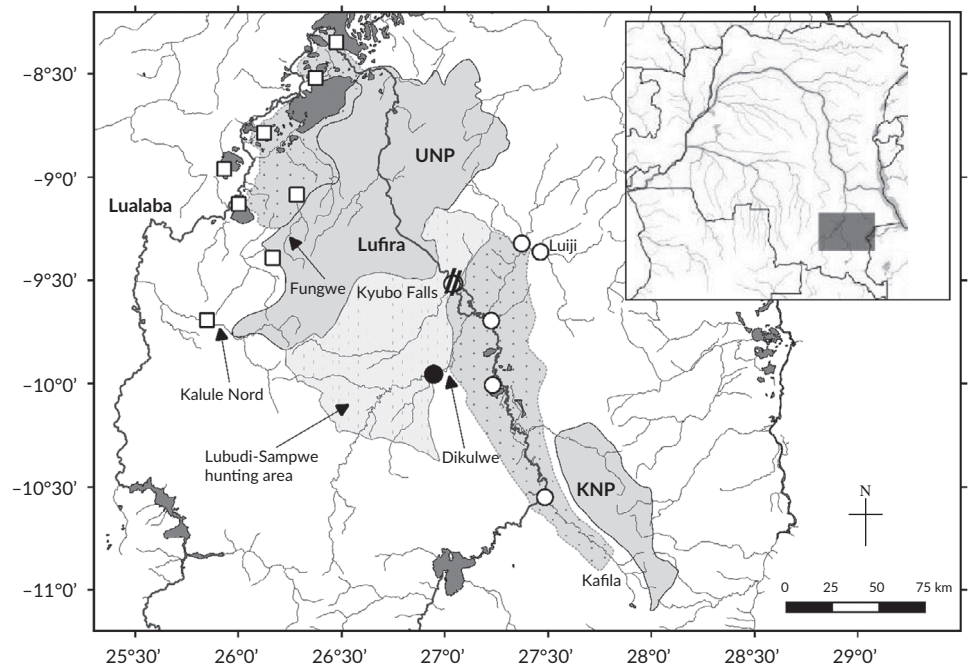
h	<i>C. aelbroecki</i>			<i>C. cubangoensis</i>			<i>C. discorhynchus</i>			<i>C. tanganicanus</i> (synonym of <i>C. discorhynchus</i> )			<i>C. lufrae</i>					
	s (n = 4)			l			pl (n = 4)			s (n = 3)			All specimens (n = 10)			All specimens (n = 45)		
	Mean ± SD	Range	Counts	163.4	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range
Post-orbital length	57.7	59.4 ± 1.5	58.1–61.3	59.7	58.5 ± 0.8	57.4–59.3	60.0 ± 1.4	56.7–63.3	60.8 ± 3.0	57.4–63.5	60.2 ± 2.8	54.9–63.5	62.1	58.7 ± 1.9	55.1–63.9			
Snout length 1 (SNL)	21.3	21.5 ± 0.9	20.5–22.5	23.1	21.3 ± 1.0	20.0–22.3	21.0 ± 1.0	18.9–23.3	20.6 ± 0.5	20.2–21.3	20.6 ± 1.2	18.8–22.7	19.2	21.6 ± 1.3	18.9–24.6			
Length of snout 2 (LSO)	39.5	43.5 ± 1.3	41.7–45.0	42.5	41.1 ± 1.6	39.7–42.7	42.6 ± 1.4	40.2–45.5	42.7 ± 1.7	41.7–44.7	42.9 ± 1.3	41.5–44.7	41.6	42.6 ± 1.7	37.4–45.9			
Length of snout 3 (LSc)	29.2	31.8 ± 0.4	31.3–32.3	31.8	29.8 ± 2.6	26.0–31.8	30.7 ± 1.3	28.0–32.9	30.1 ± 0.7	29.5–30.9	30.5 ± 0.9	29.5–31.8	29.5	31.2 ± 1.8	25.3–34.3			
Distance between nostrils	3.3	3.8 ± 0.2	3.5–4.1	4.0	3.4 ± 0.2	3.2–3.6	3.4 ± 0.3	2.3–4.0	4.1 ± 0.2	3.9–4.3	4.1 ± 0.2	3.5–4.5	3.9	3.7 ± 0.3	2.6–4.3			
Distance between nostril and eye	3.5	5.8 ± 0.4	5.3–6.2	6.3	5.8 ± 0.7	4.9–6.7	5.3 ± 0.7	3.6–6.4	4.4 ± 0.3	4.0–4.7	5.0 ± 0.5	4.0–5.7	5.5	6.3 ± 0.5	5.0–7.3			
Length of the gill opening	33.0	34.7 ± 1.0	33.7–35.9	36.4	38.2 ± 1.5	36.3–39.5	36.8 ± 1.3	34.1–39.4	36.9 ± 1.1	36.1–38.2	36.3 ± 2.4	32.3–40.4	29.3	33.3 ± 2.1	29.2–37.3			
<b>Counts</b>		<b>Median</b>	<b>Range</b>	<b>Median</b>	<b>Range</b>	<b>Median</b>	<b>Range</b>	<b>Median</b>	<b>Range</b>	<b>Median</b>	<b>Range</b>	<b>Median</b>	<b>Range</b>	<b>Median</b>	<b>Range</b>			
Dorsal-fin rays	32	31	31	32	34	31–37	34	31–36	33	31–34	34	31–34	31	30	27–32			
Anal-fin rays	26	23	22–23	25	25	24–26	24	23–26	24	23–25	25	23–25	24	23	21–25			
Pelvic-fin rays	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6			
Pectoral-fin rays	10	11	11	11	11	11	11	11	10	10	11	10–11	10	10	10			
Scales on lateral line	65	65	64–68	67	68	66–70	67	63–73	68	66–70	66	66–70	64	64	60–66			
Circumpeduncular scales	12	12	12	12	12	12	12	12	12	12	12	12	16	15	12–16			
Scales between dorsal and anal fins	29	28	25–28	28	29	28–30	29	28–31	30	30–31	29	30–31	31	31	20–34			
Scales between dorsal fin and lateral line	15	15	13–15	15	15	15–16	16	15–17	16	16	15	16–17	16	17	16–19			
Scales between pelvic fin and lateral line	15	15	13–15	16	16	15–16	15	14–17	17	15–17	16	15–17	18	16	15–18			
Teeth in upper jaw	3	5	4–5	5	5	5	5	4–7	5	5	5	4–5	3	4	2–5			
Teeth in lower jaw	6	6	6	6	6	6	6	5–7	7	7–8	6	6–8	6	5	3–7			
Total number of vertebrae				41	41	41	40	39–40					39	39	38–39			

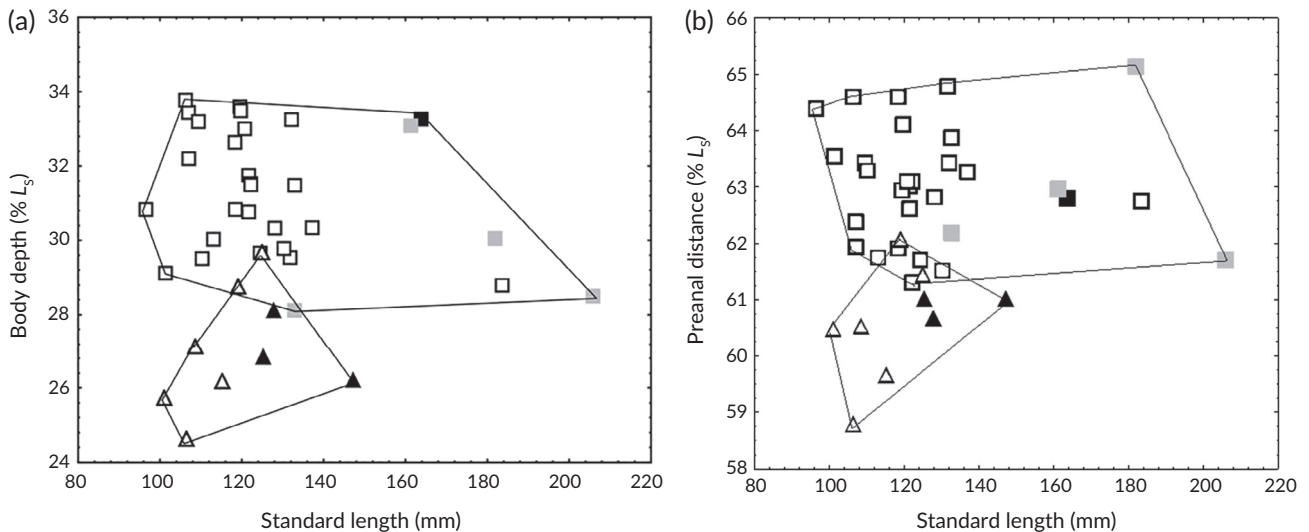
Note. h, holotype; l, lectotype; pl., paralectotype; s, syntype; SD, standard deviation. Ranges for all specimens includes the type specimens.



**FIGURE 9** Habitat diversity for *C. lufirae*: (a) Dikulwe River upstream of the road Bunkeya-Kyubo, type locality; average water depth with sections shaped small pools (09° 57' 32'' S; 26° 56' 33'' E), deep water (5 m), 23 October 2014; (b) Dikulwe River, just downstream of the bridge Bunkeya-Kyubo (09° 57' 18'' S; 26° 56' 47'' E), during fyke installation in shallow water (<0.5 m), 23 October 2014; (c) Lufira River, downstream of the Kyubo Falls on the Lower Lufira (09° 31' 02'' S; 27° 02' 09'' E), deep water (about 5–10 m), 19 October 2014; and (d) Luvilombo River below its falls and upstream of its confluence with the Lower Lufira (09° 30' 58'' S; 27° 02' 02'' E), shallow water (<0.5 m), 19 October 2014

**FIGURE 10** Distribution of *C. lufirae* in the Lufira basin, the major right bank affluent of the Upper Lualaba. UNP and KNP: Core zone, dark grey area with full contour lines; annex zone, dotted, dark grey area with contour in broken lines; Lubudi-Sampwe (LS) hunting area, dashed, light grey area hatched with full contour lines. *C. lufirae*: ●, type locality; ○, other localities; *C. discorhynchus*: □, distribution of the species in the study area





**FIGURE 11** Scatterplots of (a) body depth (%  $L_S$ ) and (b) preanal distance (%  $L_S$ ) against standard length (in mm) ( $n = 40$ ). *Cyphomyrus discorhynchus*: ■, lectotype; ■, paralectotypes of the Lower Zambezi basin; □, specimens from the Kamalondo Depression; *C. tanganicus* (currently a junior synonym of *C. discorhynchus*): ▲, syntypes; △, other specimens from some affluents of the Tanganyika basin

Based on currently available data, *C. discorhynchus* and *C. lufirae* appear to be allopatrically distributed within the Lufira River. *Cyphomyrus discorhynchus* has only been recorded from river sections below the Kamalondo Depression whereas *C. lufirae* mainly occurs above the Kyubo Falls. This suggests that the series of rapids and pools that separate the upper and lower reaches of the Lower Lufira River could have formed a barrier that prevented the dispersal of *C. discorhynchus* into the Upper Lufira. This is consistent with Poll's (1976) observations of the faunal discontinuities between the Lualaba-Upemba and the Lufira rivers.

Preliminary findings from ongoing studies suggest that the Middle Lufira contains some species within the genera *Hippopotamyrus*, *Marcusenius* and *Pollimyrus* that could also be endemic to this region (CMM personal observation, 2016), which highlights the conservation importance of this region. Currently, *C. lufirae* is considered endemic to the Middle Lufira and the upper part of the Lower Lufira basin. Unfortunately, application of the existing fish protection regulations is largely deficient in both the UNP and KNP. As a result, anthropogenic threats to their fish diversity are increasing (Abell *et al.*, 2008; Thieme *et al.*, 2005), and this especially since their large mammal fauna has already been largely decimated (Hasson, 2015; Malaisse, 1997). In addition, the distribution of the new species extends into the Lubudi-Sampwe hunting area and the annex area of the KNP, where threats due to increasing human encroachment and settlement are also rising. These are generally associated with increases in unsustainable fishing practices such as the use of mosquito nets, overfishing and habitat destruction as encountered mainly in the Kamalondo Depression of the UNP (Brown & Abell, 2005) but which also prevail in the Lufira Depression, the vast floodplain of the Middle Lufira where the new species is present (Melli & Micha, 2015). However, recently (CMM personal observation, 2017), the rigorous implementation of the sustainable management of fisheries resources by the Institut Congolais pour la Conservation de la Nature has

considerably reduced the use of prohibited fishing nets in the Lufira Depression. For the rest of the distribution of the new species in the KNP there are also strong threats to the fish fauna of the rivers surrounded by villages, especially those located at the foot of the western slope of the Kundelungu Plateau where fishing with the use of ichthyotoxic plants, such as the so-called *Buba* (*Tephrosia vogelii* Hooker *et al.* 1849), is widespread. During these practices fishing nets with small mesh sizes (about 10 mm) are used, which block the up- and downstream migration of fishes in the river which tend to escape the application of the ichthyotoxines applied. Finally, as far as there is no good surveillance of the fishing activities, the effective protection and conservation of the ichthyofauna of both the UNP and the KNP remain uncertain. It is therefore hoped that the discovery of yet another new fish species for this area further stresses the importance of both parks for fish protection and conservation.

## 5 | COMPARATIVE MATERIAL EXAMINED

### 5.1 | *Cyphomyrus aelsbroeckii* (Poll 1945)

MRAC 54990, holotype, 71.4 mm  $L_S$ ; DRC: Haut-Katanga Province, Lubumbashi (former Elisabethville), 1937, R.P Van Aelsbroeckii.

### 5.2 | *Cyphomyrus cubangoensis* (Pellegrin 1936)

MRAC P-138760 (ex. MNHN 1936-65), Syntype, 83.2 mm  $L_S$ ; Angola: Cubango (Okavango) basin. Dr. Monard (Swiss missions in Angola), 1928-29, 1932-33. MNHN 1936-0062-0064, 3 syntypes, 82.1-87.2 mm  $L_S$ ; Angola: Cubango (Okavango) basin. Dr. Monard (Swiss missions in Angola), 1936.



### 5.3 | *Cyphomyrus discorhynchus* (Peters 1852)

ZMB 3674, Lectotype, 163.7 mm  $L_S$ ; Mozambique: Lower Zambezi River; W.C. Peters; Lectotype selected by Seegers (1996: 69). ZMB 3673, 3675–3676 & 23,374, four Paralectotypes, 132.8–205.8 mm  $L_S$ ; Mozambique: Lower Zambezi River; W.C. Peters; Paralectotypes. ZSM Zam10, 101.3 mm  $L_S$ , Mozambique: Middle Zambezi just below the Victoria Falls near the beginning of Batoka Gorge: rapid, about (17°56'S; 25°51'E), 7 December 1996; Van der Bank and B. Kramer. MRAC 2016-003-P-0149-0155, 106.2–137.1 mm  $L_S$ ; DRC: UNP, Haut-Katanga Province, lake Lukanga (Katelwa fishing camp), Kamalondo Depression, Upper Lualaba (8°20'44"S; 26°28'25"E); Alt. 563 m a.s.l.; C. Mukweze, B. Katemo, E. Muyambo & D. Mfwana, 11 September 2015. MRAC 2016-003-P-0135-0140, 96.5–131.7 mm  $L_S$ ; DRC: UNP, Haut-Katanga Province, Lake Mulenda (Kyabu village), Kamalondo Depression, Upper Lualaba (8°46'23"S; 26°2'43"E); Alt. 571 m a.s.l.; C. Mukweze, B. Katemo, E. Muyambo & D. Mfwana, 2 September 2015. MRAC 2016-003-P-0141-0145, 107.0–128.0 mm  $L_S$ ; DRC: UNP, Haut-Katanga Province, Lake Upemba (specimens purchased at Misebo's market), Kamalondo Depression, Upper Lualaba. About (8°35'11"S; 26°30'43"E); Alt. 561 m a.s.l.; C. Mukweze, B. Katemo, E. Muyambo & D. Mfwana, 11 September 2015.

### 5.4 | *Cyphomyrus macrops* (Boulenger 1909)

BMNH 1899.6.27.12, holotype, 174.0 mm  $L_S$ ; DRC: Upper Congo.

### 5.5 | *Cyphomyrus psittacus* (Boulenger 1897)

BMNH 1897.9.30.26, holotype, 112.7 mm  $L_S$ ; DRC: Congo River, Stanley Falls (0°30'N; 25°12'E), W. Bentley.

### 5.6 | *Cyphomyrus smithersi* (Määr 1962) synonym of *Cyphomyrus discorhynchus* (Peters, 1852)

MRAC 183658–60, 120.7–132.9 mm  $L_S$ , southeastern Africa, Rhodesia (Zimbabwe): Chipepo River above Kariba Lake (16°49'S; 27°50'E), 01 May 1965; Matthes. MRAC 183662–63, 110.2–183.6 mm  $L_S$ , southeastern Africa, South Rhodesia (Zimbabwe): Sibilobilo (clear darea), Kariba Lake, about (16°47'S; 28°11'E), 24 April 1965; Matthes.

### 5.7 | *Cyphomyrus tanganicanus* (Boulenger 1906) synonym of *Cyphomyrus discorhynchus* (Peters, 1852)

BMNH 1906.9.8.3–4, Syntypes, 125.2–127.7 mm  $L_S$ , Sumbu and river at Msamba, Lake Tanganyika, 1906, W. Cunnington. BMNH 1906.9.8.5, Syntype, 147.1 mm  $L_S$ , Sumbu and river at Msamba, Lake Tanganyika, 1906, W. Cunnington. MRAC 1992.081.P.0071, 106.4 mm  $L_S$ , Tanzania: Ulwile Island, northern shore, Lake Tanganyika (7°27'S;

30°34'E), 1992; Expedition 1992. MRAC 1992-081-P-0163, 101.0 mm, Tanzania: Ulwile Island, northern shore, Lake Tanganyika (7°27'S; 30°34'E), 1992; Expedition 1992. MRAC P-126349, 85.7 mm  $L_S$ , DRC: Uvira, Lake Tanganyika (3°24'S; 29°8'E), 1958; Expedition 1992. MRAC 91-034-P-0180-0183, 115.2–124.9 mm  $L_S$ , Burundi: Bujumbura, Lake Tanganyika (specimens purchased at the market) (3°23'S; 29°22'E), October 12, 1994; L. De Vos. MRAC P-190342, 108.6 mm, Zambia: Liemba jetty (Mpulungu), Lake Tanganyika (8°46'S; 31°7'E), 11 July 1967; H. Matthes.

### 5.8 | *Cyphomyrus wilverthi* (Boulenger 1898)

MRAC 133, syntype, 239.9 mm  $L_S$ ; DRC: Upoto, Upoto 1896, Wilverthi.

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### AUTHORS' CONTRIBUTIONS

CMM, BMK and EV were responsible for the fieldwork, fish identification and study design, and wrote the first and subsequent revised versions of the manuscript. In addition, EV supervised the research and critically revised the final version of the manuscript. ED was mainly responsible for the molecular work, sequence data analyses and writing and supervision of the paragraphs related to this part of the paper. All authors discussed, read and rewrote parts of the manuscript, and approved its final version.

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