

## The Victoria Falls, a species boundary for the Zambezi Parrotfish, *Cyphomyrus discorhynchus* (Peters, 1852), and the resurrection of *Cyphomyrus cubangoensis* (Pellegrin, 1936) (Mormyridae: Teleostei)

Bernd Kramer<sup>a\*</sup> and F. Herman Van der Bank<sup>b</sup>

<sup>a</sup>Zoological Institute of the University of Regensburg, Universitätsstrasse 31, D-93040 Regensburg, Germany; <sup>b</sup>Department of Zoology, University of Johannesburg, Johannesburg, South Africa

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*Cyphomyrus discorhynchus* occurs in the Zambezi River and in the linked systems of the Kwando and the Okavango. We collected specimens from both above and below the Victoria Falls and recorded Electric Organ Discharges. We found a marked degree of anatomical differentiation among the specimens from the Zambezi delta to the Victoria Falls that represents a subspecific, geographical cline, reflecting the great length (1400 km) and high ecological diversity of that river section (Lower and Middle Zambezi). We confirm that the populations above the Falls (i.e. Upper Zambezi, Kwando and Okavango) are differentiated from those below, possessing fewer dorsal fin rays (a median of 30–31 rather than 33–34). The waveforms of the electric organ discharge pulses have four phases and show geographic variation but were briefer for specimens from below the Falls. We resurrect *Cyphomyrus cubangoensis* (Pellegrin, 1936) for the Upper Zambezi/Kwando/Okavango system.

**Keywords:** allopatric speciation; parapatric; geographic cline; electric organ discharges; southern Africa

### Introduction

The genus *Cyphomyrus* Myers, 1960 includes a few species inhabiting the Congo and the Zambezi with a rounded or arched back and a long dorsal fin, the origin of which is well in front of the anal fin (Figure 1). It has been synonymized with the genus *Hippopotamyrus* Pappenheim, 1906 by Taverne (1971a), but Van der Bank and Kramer (1996) proposed that *Cyphomyrus discorhynchus* (Peters, 1852) be reinstated on the basis of marked morphological and molecular genetic (allozyme) differentiation from sympatric species of the *Hippopotamyrus ansorgii* complex, confirmed by mitochondrial DNA sequence analysis (Kramer et al. 2004; Kramer and Swartz 2010). Sullivan et al. (2000) and Lavoué et al. (2003) have also shown that the genus *Hippopotamyrus* (*sensu* Taverne) is polyphyletic, with two lineages, supporting *Cyphomyrus* Myers. Although the systematics of mormyrids has made great progress through these and many other molecular-genetic studies that have appeared in recent years (e.g. Lavoué et al. 2000, 2010; Sullivan et al. 2004; Feulner et al. 2007), the problem of distinguishing between *Hippopotamyrus* and *Cyphomyrus* has not been resolved. At present the two genus names coexist in an unclear manner for some of the fish pertaining

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\*Corresponding author. Email: bernd.kramer@biologie.uni-regensburg.de

to *Cyphomyrus* Myers, 1960, awaiting a revision of the genus *Hippopotamyus* (see Eschmeyer 2010). We will use *Cyphomyrus* rather than *Hippopotamyus* for fish of the *C. discorhynchus* complex in the present paper.

The type locality of the Zambezi parrotfish, *C. discorhynchus*, is on the Lower Zambezi River, but it also occurs in the Buzi and Pungwe rivers, the middle and upper Zambezi, the Okavango and Cunene. The species is absent from the Kafue System but has been observed in the upper Congo and in Lakes Tanganyika and Malawi (Skelton 2001; Scott et al. 2006). This is a patchy distribution over a huge area of southern Africa that calls for a critical comparison of allopatric populations.

The Victoria Falls divide the fish fauna of the Zambezi into a species-rich upper section and a lower section that holds generally fewer, and also different, fish species (Jubb 1958; Balon 1974; Skelton 2001). There are examples of sibling species pairs with the geographical barrier believed to be formed by the Victoria Falls, such as the Western and Eastern Bottlenoses, *Mormyrus lacerda* Castelnau, 1861 (upper Zambezi) and *Mormyrus longirostris* Peters, 1852 (middle and lower Zambezi), or the two bulldog fish species, *Marcusenius macrolepidotus* (Peters, 1852) and *Marcusenius altisambesi* (Kramer et al., 2007). Examples of species occurring in the lower and middle, but not the upper, Zambezi are the Zambezi electric catfish, *Malapterurus shirensis* Roberts, 2000 and the cornish jack, *Mormyrops anguilloides* (Linnaeus, 1758). Balon (1974) and Winemiller (1991) have questioned the effectiveness of the Victoria Falls as a barrier for downstream invasions by Upper Zambezi fish, whereas all authors seem to agree that invasions upstream over a barrier of about 100 m (107 m according to www.World-Waterfalls.com) are unlikely. Minshull (2010) reports the occurrence of certain Upper Zambezi species below the Falls, such as *Marcusenius altisambesi* and *Mormyrus lacerda* (whether this is evidence of a regularly occurring phenomenon has still to be confirmed; J. Minshull, personal communication). Upper Zambezi fish that are adapted to the floodplain ecology of what has been classified a reservoir-river might not survive well in the unfavourable environment of the Middle Zambezi, which is a sandbank-river (strong current, rapid change in water level, little cover).

We sampled parrotfish from the Upper Zambezi and its tributary, the Kwando River, from the Zambezi just below the Victoria Falls, and a few specimens from the type locality, Tete on the Lower Zambezi (Figure 2). All of these fish were studied for their electric organ discharges (EODs) and anatomy. We used collection specimens from the Lower Zambezi, the Okavango and Lake Tanganyika for anatomical comparisons. The main question was to ascertain the taxonomic status of the fish from the Upper Zambezi System including the Okavango. We specifically paid attention to the possibility of the Victoria Falls representing a geographical barrier associated with differentiation within *C. discorhynchus*.

## Materials and methods

### *Morphology*

Seventeen anatomical measurements (Figure 3) and four counts were performed on 134 specimens from various origins in Mozambique, Zimbabwe, Namibia, Botswana, Angola and Zambia: PDL, predorsal length (distance from the tip of the snout to the dorsal fin origin); PAL, distance from tip of snout to anal fin origin; LD, dorsal fin length; LA, anal fin length; pD, distance from dorsal fin origin to end of caudal

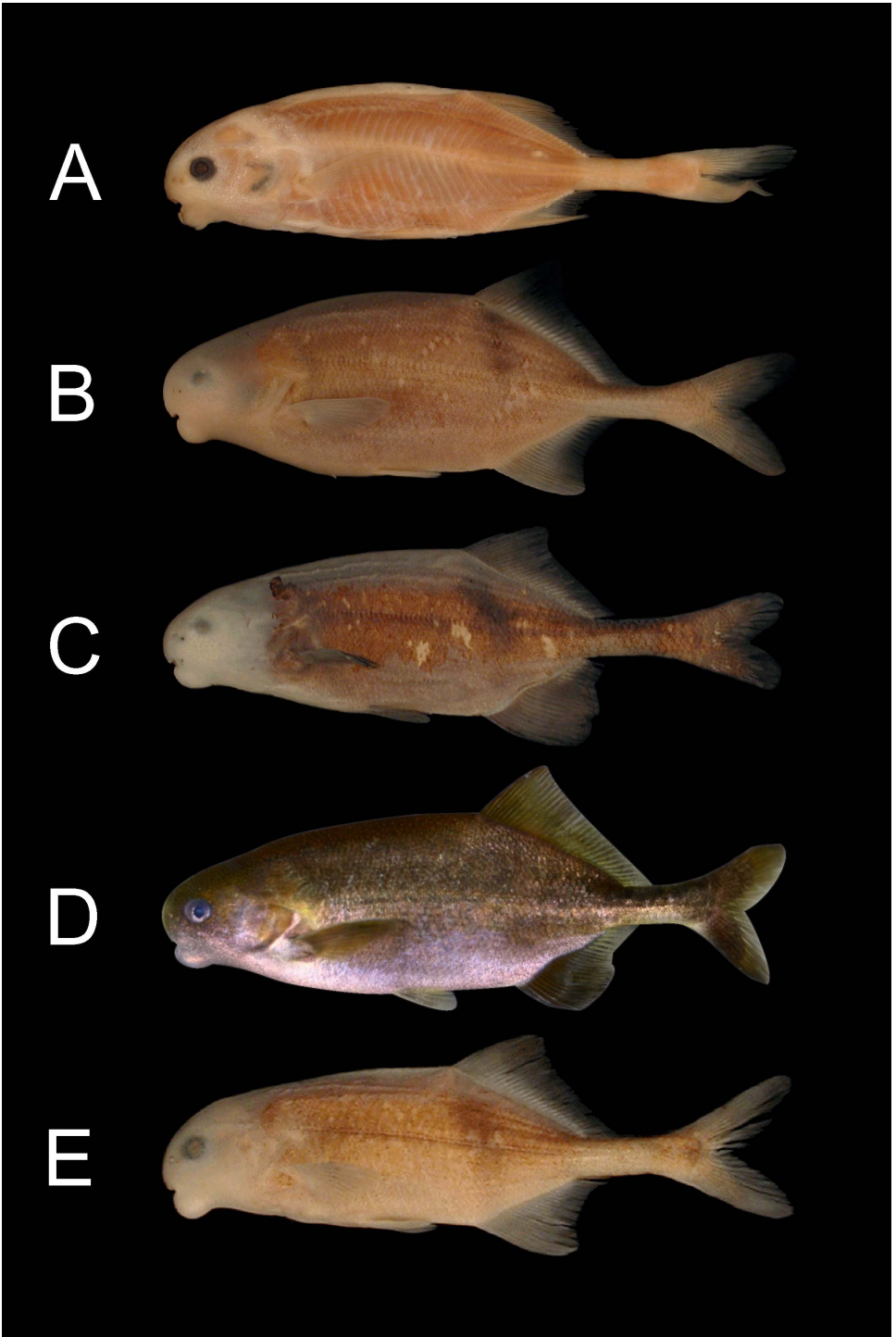




Figure 1. Members of the *Cyphomyrus discorhynchus* species complex. (A) *Marcusenius cubangoensis* Pellegrin 1936, Upper Okavango River, Angola (NMB 5216, syntype); (B) *Cyphomyrus cubangoensis* (Pellegrin, 1936), Namibia: province Kavango: Okavango River (SAIAB 20384 specimen R1); (C) *C. cubangoensis* (Pellegrin, 1936), Namibia: Caprivi Strip: Kwando River:

peduncle; CPL, length of caudal peduncle (end of anal fin base to mid-base of the caudal fin); CPD, depth of caudal peduncle (the least vertical distance across the caudal peduncle); LSo, length of snout (distance from the tip of the snout to the posterior orbital rim of the eye); LSc, length of snout (distance from the tip of the snout to the centre of the eye); HL, head length (distance from the tip of the snout to the furthest bony edge of the operculum); Na, distance between the pair of nares on one side (from centre to centre); OD, eye diameter defined by the orbital rims; LPF, length of the pectoral fins; PPF, distance from the origin of the pelvic fin to the origin of the anal fin (some specimens); SL, standard length (distance between the tip of the snout to the mid-base of the caudal fin); BD, body depth (the greatest vertical distance across the body); TL, total length (distance from the tip of the snout to the end of the caudal fin); nD, number of dorsal fin rays; nA, number of anal fin rays; SPc, number of scales around the caudal peduncle; SLS, number of scales in a linear series along the lateral line row, as detailed in Skelton (2001: 67); SLS, range of accuracy  $\pm 2$  counts.

Abbreviations used to represent institutions and collections cited follow Leviton et al. (1985) and Fricke and Eschmeyer (2011). Specimens examined were initially identified using dichotomous keys in Bell-Cross and Minshull (1988) and Skelton (2001), which are considered effective for fish populations occurring in southern Africa.

The male sex was inferred when the anal fin base showed a kink, a character also present in many other species of mormyrids. Females and juveniles show no such kink (Skelton 2001).

### *Electric organ discharges*

The EODs of live fish were recorded in the field immediately after capture. Measurements were taken in a 37-litre plastic aquarium filled with water taken from the river where the fish was collected. Conditions in the aquarium were kept constant throughout the analysis to exclude the possibility that water quality (especially conductivity) could affect EOD measurements.

Temperature ( $\pm 0.1^\circ\text{C}$ ) and water conductivity ( $\pm 1 \mu\text{S cm}^{-1}$ ) were constantly monitored using an electronic apparatus (LF318 WTW, Wissenschaftlich Technische Werkstätten GmbH, 82362 Weilheim, Germany). Fish were placed between a pair of carbon rod electrodes that were connected to a differential amplifier with a variable gain (up to  $\times 10$ ; 0.2 Hz . . . 100 kHz; filter slopes,  $-3$  dB per octave; electronics workshop, Biology Department, University of Regensburg). Amplifier output was recorded with a digital storage oscilloscope (100 MHz/9 bit/10 000 points per sweep) and data were numerically transferred onto disk via digital interface. Usually eight traces per fish were recorded. All the field equipment was battery operated.

Figure 1. (Continued) Kongola Bridge (SAIAB 96761); (D) *C. cubangoensis* (Pellegrin, 1936), Namibia: Caprivi Strip: Upper Zambezi River: Katima Mulilo (live photograph in aquarium by Ellen Fröhlich); (E) *C. cubangoensis* (Pellegrin, 1936), Namibia: Caprivi Strip: Upper Zambezi River: Katima Mulilo (SAIAB 96693); (F) *Cyphomyrus discorhynchus* (Peters, 1852), Zambia: Middle Zambezi River: Batoka Gorge, Rapid # 6 (SAIAB 96688); (G) *C. discorhynchus* (Peters, 1852), Mozambique: Lower Zambezi River: Tete (ZSM 38644); (H) *C. discorhynchus* (Peters, 1852), Mozambique: Lower Zambezi River: delta region at Marromeu (SAIAB 60874, specimen R1); (I) *Marcusenius tanganicus* Boulenger, 1906, Zambia: Lake Tanganyika: Msamba (BMNH 1906.9.8.3–4 specimen R2, syntype).



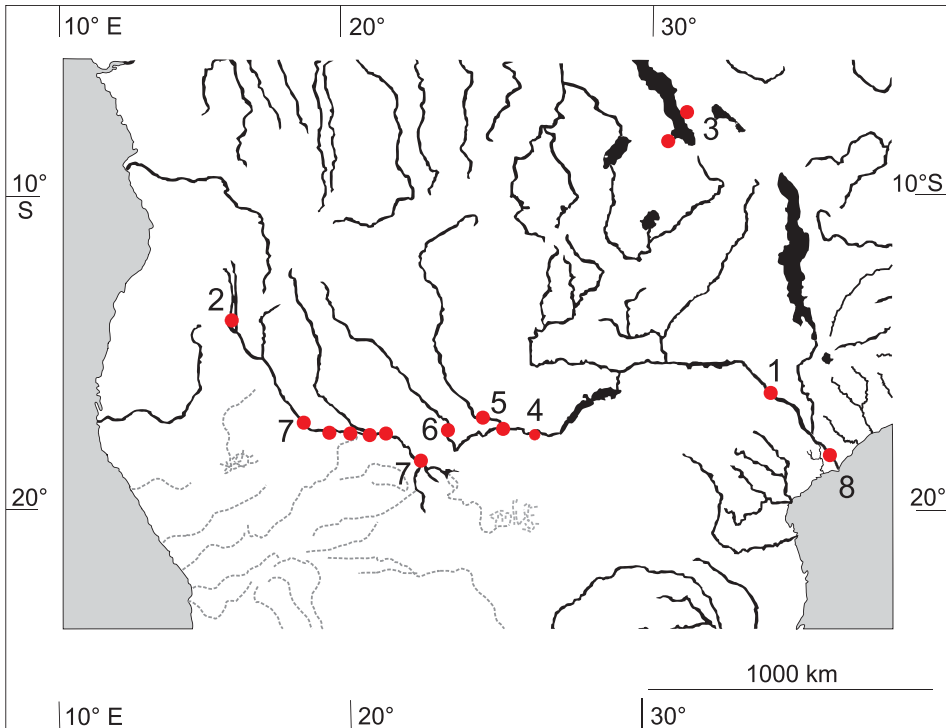


Figure 2. Geography of the study area. (1) Type locality for *Cyphomyrus discorhynchus* (Peters, 1852), Tete on the Lower Zambezi. (2) Type locality of *Marcusenius cubangoensis* Pellegrin, 1936 on or close to the Cubango River in Angola. (3) Two possible sampling localities (guessed from original description) for *Marcusenius tanganicanus* Boulenger, 1906 from the Tanganyika Lake. (4) *Cyphomyrus discorhynchus* from just below the Victoria Falls. (5) Specimens from the Upper Zambezi at Katima Mulilo, Caprivi Strip, Namibia. (6) Specimens from the Kwando River, Caprivi Strip, Namibia. (7) Range of specimens from the Okavango River, Kavango Province, Namibia, and Okavango delta, Botswana. (8) *Cyphomyrus discorhynchus* from Marromeu, Lower Zambezi, delta region.

Custom-designed computer programs were used for analysis of EODs (programmed using a software package for signal analysis, FAMOS v5). When necessary, EOD duration was corrected to 25°C using a Q10 value of 1.5 (Kramer and Westby 1985) before data analysis.

The EOD waveform variables can be defined as follows (compare with Figure 4): P1amp, peak amplitude of positive P1 phase (i.e. from baseline to peak, which is equal to 1 V by definition); N0amp, P2amp, negative and positive peak amplitudes of pre- and post potentials, respectively; N1amp, negative peak amplitude of N1 phase of EOD re: P1amp = 1; N0dur, P1dur, N1dur, durations of respective phases; PIN1sep, separation (or interval) between the peaks of the P1 and N1 phases; P1area, N1area, areas under the P1 and N1 phases; EODdur, total EOD duration. Durations in microseconds or milliseconds, as indicated; amplitudes in relative Volts (re: P1-phase amplitude = 1). Area-under-curve measurements: dimension (V × microseconds).

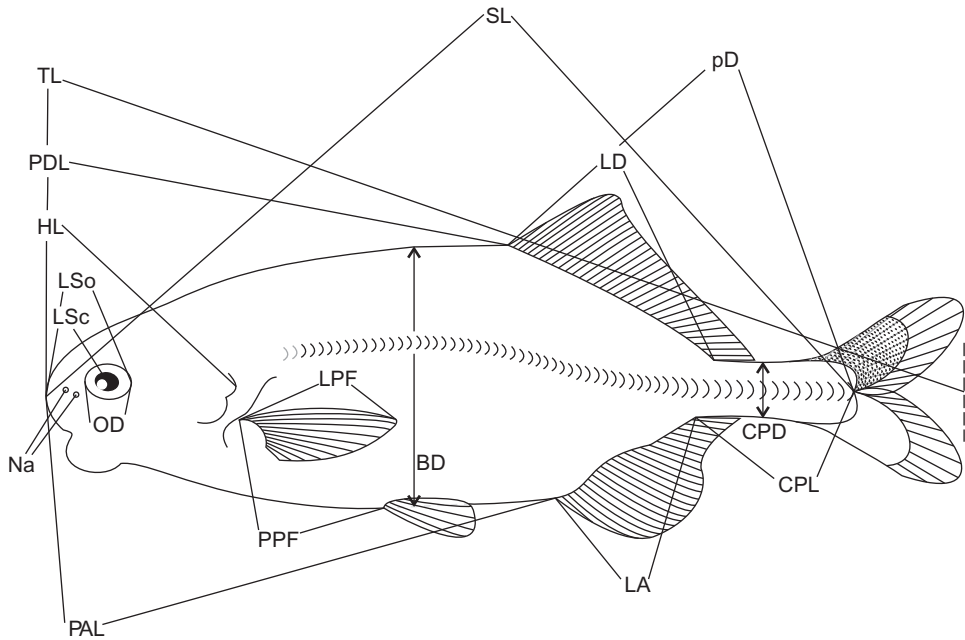


Figure 3. Morphological characters and how they were measured (for abbreviations, see Material and Methods).

The start of the initial P0 phase and the end of the terminal P2 phase were determined at a threshold level of 5% of P1amp; other phases start and end between zero crossings.

A Fast Fourier Transform routine provided by FAMOS performed amplitude spectra of single EOD pulses. Analogue-to-Digital (A/D) sampling rates were reduced to between 100 and 125 kHz. The number of data points for Fast Fourier Transform analysis was  $2^{19}$ , obtained by extending the baseline with zeros such that a single EOD per record was centred (Davis and Hersh 1980; Bracewell 1986; Keuper 1988). Frequency resolution was  $< 0.24$  Hz. The peak power frequency (PPF in Hz) was determined from these spectra.

Subsequent to EOD recording, fish were killed with an overdose of the anaesthetic 2-phenoxy-ethanol. SL was measured with vernier callipers before fixing the specimen in 10% formalin for morphological studies.

### **Statistical analyses**

Principal component analyses (PCA) on correlations among anatomical characters were used to test differences in body shape among populations, because it does not require *a priori* assumptions about taxonomic groups. Analyses of variance (ANOVA) were performed to test the hypotheses of no difference between samples of different origins for each character separately. Multivariate analyses of variance (MANOVA) were carried out to prevent overestimating the differentiation in testing the hypothesis of no morphological difference between fish from different origins (McGarigal et al.

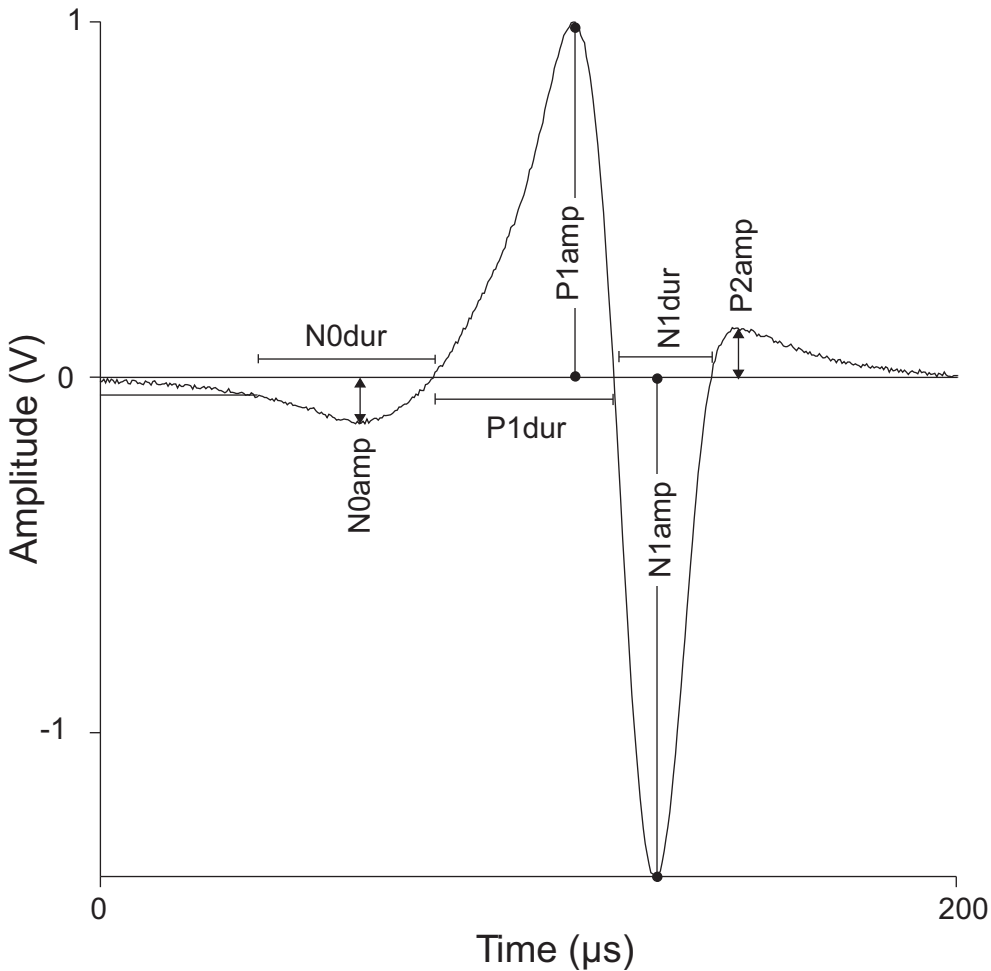


Figure 4. Characters of an Electric Organ Discharge (EOD) pulse of a *Cyphomyrus cf. discorhynchus* and how they were defined. P1amp was normalized to 1 Volt by definition.

2000). Probability ( $p$ ) values were two-tailed unless otherwise stated. We determined the component loadings, i.e. the principal component structure, for interpreting the principal components in terms of the anatomical characters (McGarigal et al. 2000). We followed Tabachnick and Fidell (2007) to interpret the significance of component loadings. These authors recognize five levels of significance: loadings  $> 0.32$  or  $\leq 0.32$  are poor,  $> 0.45$  or  $\leq 0.45$  are fair,  $> 0.55$  or  $\leq 0.55$  are good,  $> 0.63$  or  $\leq 0.63$  are very good, and  $> 0.71$  or  $\leq 0.71$  are excellent. These benchmarks account for 10%, 20%, 30%, 40% and 50% of the variance in the component. We also performed discriminant function analyses (DFA) to find the best separation among the specimens from different origins in multidimensional space, using JMP v. 9 software (SAS Institute, Cary, NC, USA, 2007). The best result was obtained by stepwise variable selection, as measured by the smallest  $-2\text{LogLikelihood}$  (that is, minus two times the natural log of the likelihood function evaluated at the best-fit parameter estimates).



**Material examined***Cyphomyrus discorhynchus* (Peters, 1852)

- SAIAB 96691(2), ZSM 38644(2), four specimens, Mozambique: Lower Zambezi: Tete, 16°09'19.3" S, 033° 36'01.0"E, 119 m altitude, 4 August 2003, field nos Disco 1–3, Disco00011, SL 11.4–13.3 cm, water: 134.8  $\mu$ S/cm at 20.5°C on 3 August 2003, 6 a.m., coll. F.H. Van der Bank and B. Kramer,
- SAIAB 96680, SAIAB 96681(6), SAIAB 96688(7), ZSM 38639, ZSM 38640(5), ZSM 38641(7), 27 specimens, field nos Zam01–Zam08, Zam10–Zam15, Zam16a, Zam16b, Zam17–Zam21, Zam23–Zam28, SL 9.4–14.4 cm, Zambia: Middle Zambezi just below the Victoria Falls near the beginning of Batoka Gorge: rapid no. 6, about 17°56' S 25°51' E, 6–8 December 1996, water: 81  $\mu$ S/cm at 27.6°C on 7 December at 09.00, coll. F.H. Van der Bank and B. Kramer,
- SAIAB 96689(3), ZSM 38642(3), field nos Zam29–Zam32, Zam31a, Zam33a, SL 11.3–13.7 cm, Zambia: Middle Zambezi: rapid no. 23 further downstream, 9 December 1996, water: 81.6  $\mu$ S/cm at 28.1°C on 9 December at 07:40 h, coll. F.H. Van der Bank and B. Kramer,
- SAIAB 96690, ZSM 38643(2), field nos Zam33b, Zam34, Zam36, SL 11.8–12.7 cm, Zambia: Middle Zambezi: rapid no. 25 still further downstream, 11 December 1996, water: 81.9  $\mu$ S/cm at 27.6°C on 11 December at 08:14 h, coll. F.H. Van der Bank and B. Kramer.
- SAIAB 60874, 19 (of 23) specimens, SL 6.6–9.8 cm, Mozambique: Zambezi System: Zambezi River: island bank off the Marromeu harbour, 18°17'08.63" S, 35°56'58.83" E, 3 August 1999, Fishermen and R. Bills.
- BMNH 1906.9.8.3–4 (2 syntypes) *Marcusenius tanganicus* Boulenger 1906, Zambia: Lake Tanganyika: Sumba (Sumbu?), Cunnington, SL 12.7–12.8 cm.
- BMNH 1906.6.9.8.5 (1 syntype), *Marcusenius tanganicus* Boulenger 1906, Tanzania: Lake Tanganyika: Msamba, Cunnington. SL 15.0 cm.

*Cyphomyrus cubangoensis* (Pellegrin, 1936)

- NMB 5216 (1 syntypes) *Marcusenius cubangoensis* Pellegrin 1936, SL 7.7 cm, purchased by A. Monard, fleuve Cubango (Okavango) River, Angola.
- MHNG 858.85 (1 syntypes) *Marcusenius cubangoensis* Pellegrin 1936, SL 7.6 cm, Kuvango (Okavango) River, Angola. Expdt. Suisse, purchased by A. Monard.
- MRAC 138760 (ex MHNH 1936-65), *Marcusenius cubangoensis* Pellegrin 1936, SL 8.4 cm, donated by A. Monard, Coubango (Okavango) River, Angola, 1928–29, 1932–33.
- ZSM 38645, ZSM 38646, two specimens from Namibia: Upper Zambezi: Katima Mulilo, approx. 17°29'30" S, 24°16'18" E, 12–13 September 1993, field nos Fish49, Fish54, respectively, SL 3.9–5.0 cm, water conductivity and temperature, 81  $\mu$ S/cm, 21.8°C, coll. F.H. Van der Bank and B. Kramer,
- ZSM 38647, one specimen from Namibia: Upper Zambezi: Lisikili, 17°33' S, 24°29' E, 6 March 1994, field no. L23isi, SL 12.4 cm, 6 March 1994, water conductivity and temperature, 56.1  $\mu$ S/cm, 26.8°C, coll. F.H. van der Bank and B. Kramer,
- SAIAB 96692(2) (field nos Ka57, Ka59), SAIAB 96693(3) (Ka60, Ka62, Ka63), ZSM 38655 (Ka65), SL 5.5–6.8 cm, six specimens from Namibia: Upper Zambezi:

- Katima Mulilo: Wenela, 17°29'21.5'' S, 24°15'33'' E, 2–5 April 1996, water conductivity and temperature, 66  $\mu\text{S}/\text{cm}$ , 25.9°C, coll. F.H. Van der Bank and B. Kramer,
- SAIAB 96694(4) (field nos Wen03, Wen06, Wen08, Wen11), SAIAB 96695 (R1), ZSM 38648 (Wen04), ZSM 38648 (Wen07), ZSM 38648 (Wen09), ZSM 38649 (Wen12), ZSM 38650 (Wen20), SL 4.2–6.4 cm, 10 specimens from Namibia: Upper Zambezi: Katima Mulilo: Wenela, same coordinates, 23–27 August 1999; water conductivity and temperature, 84.4  $\mu\text{S}/\text{cm}$ , 22°C, coll. F.H. Van der Bank and B. Kramer,
- SAIAB 96696 (field no. 4Fish), one specimen, SL 4.8 cm, from Namibia: Caprivi Strip: Kwando River: Nkasa Island in Mamili National Park, 18°27' S, 23°42' E), 8 September 1993, water conductivity and temperature 108  $\mu\text{S}/\text{cm}$ , 18–19°C, coll. F.H. Van der Bank and B. Kramer,
- SAIAB 96697(2) (field nos N99ka, N99bka), ZSM 38651 (N80ka), ZSM 38652 (N99aka), four specimens, SL 10.3–11.1 cm, from Namibia: Caprivi Strip: Kwando River: Nakatwa in Mudumu National Park (18°06' S, 23°23' E), 11–12 March 1994, water conductivity and temperature, 130  $\mu\text{S}/\text{cm}$ , 24.9°C, coll. F.H. Van der Bank and B. Kramer,
- SAIAB 96709 (field no. Kon13g), ZSM 38653 (Kon14g), ZSM 38653 (Kon20g), three specimens, SL 3.9–5.7 cm, from Namibia: Caprivi Strip: Kwando River: Kongola Bridge, 17°47'26.7'' S, 23°20'40'' E, 25 August 1999, water conductivity and temperature, 236  $\mu\text{S}/\text{cm}$ , 19°C, coll. F.H. Van der Bank and B. Kramer,
- SAIAB 96761(2) (field nos Kon03g, Kon11g), ZSM 38654 (Kon12g), three specimens, SL 8.0–9.9 cm, from Namibia: Caprivi Strip: Kwando River: Kongola Bridge, 17°47'26.7'' S, 23°20'40'' E, 24 January 2001, water conductivity and temperature, 160  $\mu\text{S}/\text{cm}$ , 26.6°C, coll. F.H. Van der Bank and B. Kramer,
- SAIAB 18619, one specimen, SL 5.5 cm, Botswana: Okavango System: Nxamaseri side channel; 1 km downstream of P.J.'s Camp, 18.6167° S, 22.0833° E, 13 February 1983, coll. M.N. Bruton,
- SAIAB 18756, SL 6.9 cm, one specimen, Botswana: Okavango System: Nxamaseri tributary: 1 km from confluence with Okavango, 16 February 1983, coll. M.N. Bruton,
- SAIAB 20134, one specimen, SL 6.0 cm, Namibia: Okavango System: Okavango River: Mbambi Clinic, 17°58'00'' S, 21°00'00'' E, 7 March 1984, coll. P. Skelton,
- SAIAB 20254, three specimens, SL 4.1–5.7 cm, Namibia: Okavango System: Okavango River: Mkena, 18°00'00'' S, 20°52'00'' E, 6 March 1984, coll. P. Skelton,
- SAIAB 20367, one specimen, SL 11.1 cm, Namibia: Okavango System: Okavango River: Rundu, 17°53'00'' S, 20°15'00'' E, 2 March 1984, coll. P. Skelton,
- SAIAB 20384, three specimens, SL 6.3–11.3 cm, Namibia: Okavango System: Okavango River: Mupapamu Village, 17°53'00'' S, 20°15'00'' E, 3 March 1984, coll. P. Skelton,
- SAIAB 20406, two specimens, SL 5.9–9.9 cm, Namibia: Okavango System: Okavango River: Rundu, 2 March 1984, coll. P. Skelton,
- SAIAB 20492, four specimens, SL 7.7–11.6 cm, Namibia: Okavango System: Okavango River: Ombarumba, 17°57'00'' S, 20°28'00'' E, 4 March 1984, coll. P. Skelton,
- SAIAB 27379, one specimen, SL 7.3 cm, Namibia: Okavango River: Kahenge, 17°40'00'' S, 18°40'00'' E, 16 July 1987, coll. B. van der Waal,

SAIAB 37005, two specimens, SL 4.8–5.2 cm, Namibia: Okavango System: Okavango River: Rundu Tower, 17°52'00" S, 19°43'00" E, 8 July 1986, coll. G. Timothy, G. Merron,

SAIAB 44906, two specimens, SL 4.5–5.0 cm, Namibia: Okavango System: Okavango River: Mashane Rapids, 15°53'00" S, 20°13'00" E, 1 August 1994, coll. C. Hay,-  
SAIAB 45465, 17 specimens, SL 9.2–12.9 cm, Namibia: Zambezi System: Upper Zambezi River: Impalila Island, 17°47'00" S, 025°15'00" E, transferred from Transvaal Museum.

## Results

### Anatomical comparisons

An inspection of the anatomical data suggested that there are two groups of Zambezi parrotfish: an eastern group including the samples from the type locality, Tete on the Lower Zambezi, that is characterized by a long dorsal fin and a median 33 or 34 dorsal fin rays, and a group west of and above the Victoria Falls with a shorter dorsal fin and fewer rays (a median 30 or 31; see Appendix A, Table A1). Therefore, the present state of a single species of *C. discorhynchus* recognized for the whole of the Zambezi/Okavango system appeared questionable, especially as a critical comparison of allopatric populations had not been made.

The first question was whether or not the sample from the Zambezi delta region at Marromeu (Mozambique: LZ-Marr) was differentiated from that of the type locality that is also located on the Lower Zambezi (Tete, Mozambique: LZ-T; Table 1). The MANOVA that included the Upper Zambezi sample for comparison with the two Lower Zambezi samples, showed significant differentiation among the three samples ( $p < 0.0001$ ; Table 1). Ten characters out of the 15 included differed significantly among samples in univariate ANOVAs ( $p \leq 0.0154$ ; Table 1). Post-hoc tests for each character revealed which ones of the three possible paired comparisons contributed to the significant individual ANOVA results. Significant differences occurred for the comparisons of the two Lower Zambezi samples with the Upper Zambezi samples (in

Table 1. MANOVA on morphology of members of *Cyphomyrus discorhynchus* species complex from the Zambezi River.

	LD/ SL	LA/ SL	PPF/ SL	pD/ SL	CPL/ SL	CPD/ CPL	LSc/ HL	BD/ SL	nD	nA
MANOVA					<b>&lt;10<sup>-4</sup></b>					
ANOVA	<b>&lt;10<sup>-4</sup></b>	<b>&lt;10<sup>-4</sup></b>	<b>&lt;10<sup>-4</sup></b>	<b>&lt;10<sup>-4</sup></b>	0.0103	<b>10<sup>-4</sup></b>	0.0154	<b>&lt;10<sup>-4</sup></b>	<b>&lt;10<sup>-4</sup></b>	<b>&lt;10<sup>-4</sup></b>
post tests <sup>1</sup>										
LZ-T,LZ-M										
UZ,LZ-M	<b>&lt;0.01</b>	<b>&lt;0.01</b>	<b>&lt;0.01</b>	<b>&lt;0.01</b>	<0.05	<b>&lt;0.01</b>	<0.05	<b>&lt;0.01</b>	<b>&lt;0.01</b>	<b>&lt;0.01</b>
UZ,LZ-T	<b>&lt;0.01</b>	<b>&lt;0.01</b>			<0.05		<b>&lt;0.01</b>	<0.05	<b>&lt;0.01</b>	

MANOVA  $P$  value, same for Wilk's Lambda, Roy's Greatest Root, Hotelling Lawley Trace and Pillai Trace Tests;  $F_{\geq 10,48} \geq 8.147$ . Based on ten variables out of 15 that were significant in univariate ANOVAs (nonsignificant: PDL/SL, PAL/SL, HL/SL, SPc, SLS). ANOVAs,  $F_{2,56} \geq 4.502$ . For abbreviations of characters, see Material and methods.<sup>1</sup>) Games Howell test. LZ-T, Lower Zambezi at Tete (type locality;  $n = 4$ ); LZ-M, Lower Zambezi at Marromeu ( $n = 19$ ), UZ, Upper Zambezi ( $n = 36$ ).  $P$  values  $< 0.01$  in bold font.

eight and four characters at  $p < 0.01$  for the Marromeu and the Tete samples, plus two and two at  $p < 0.05$ , respectively); no significant differences were found among the paired comparisons between the two Lower Zambezi samples (Table 1). Both PCA and DFA confirmed the association of the two Lower Zambezi samples and joint separation from the Upper Zambezi samples along Principal Component 1 and Canonical 1 (Figure 5A). Therefore, we regard the sample from Marromeu ( $n = 19$ ) as also representing *C. discorhynchus* (Peters, 1852), as do those from the type locality ( $n = 4$ ), and will use them as a reference for that species for their greater sample size. Any barriers for the movement of fish are unknown between these two localities on the Lower Zambezi, despite their considerable separation (about 400 km) but only moderate difference in altitude (Tete is about 120 m above sea level in contrast to  $> 900$  m for the upper edge of the Victoria Falls).

On the basis of a MANOVA over all groups of fish with sample size  $n \geq 11$  studied in the present paper the hypothesis of no difference among them was rejected ( $p < 0.0001$ ; Table 2). Significant differentiation among the groups was observed in 14 out of the 15 characters entered in the analysis (ANOVAs,  $p \leq 0.016$ , Table 2). Post-hoc tests identified the pairs of groups that differed significantly in certain characters.

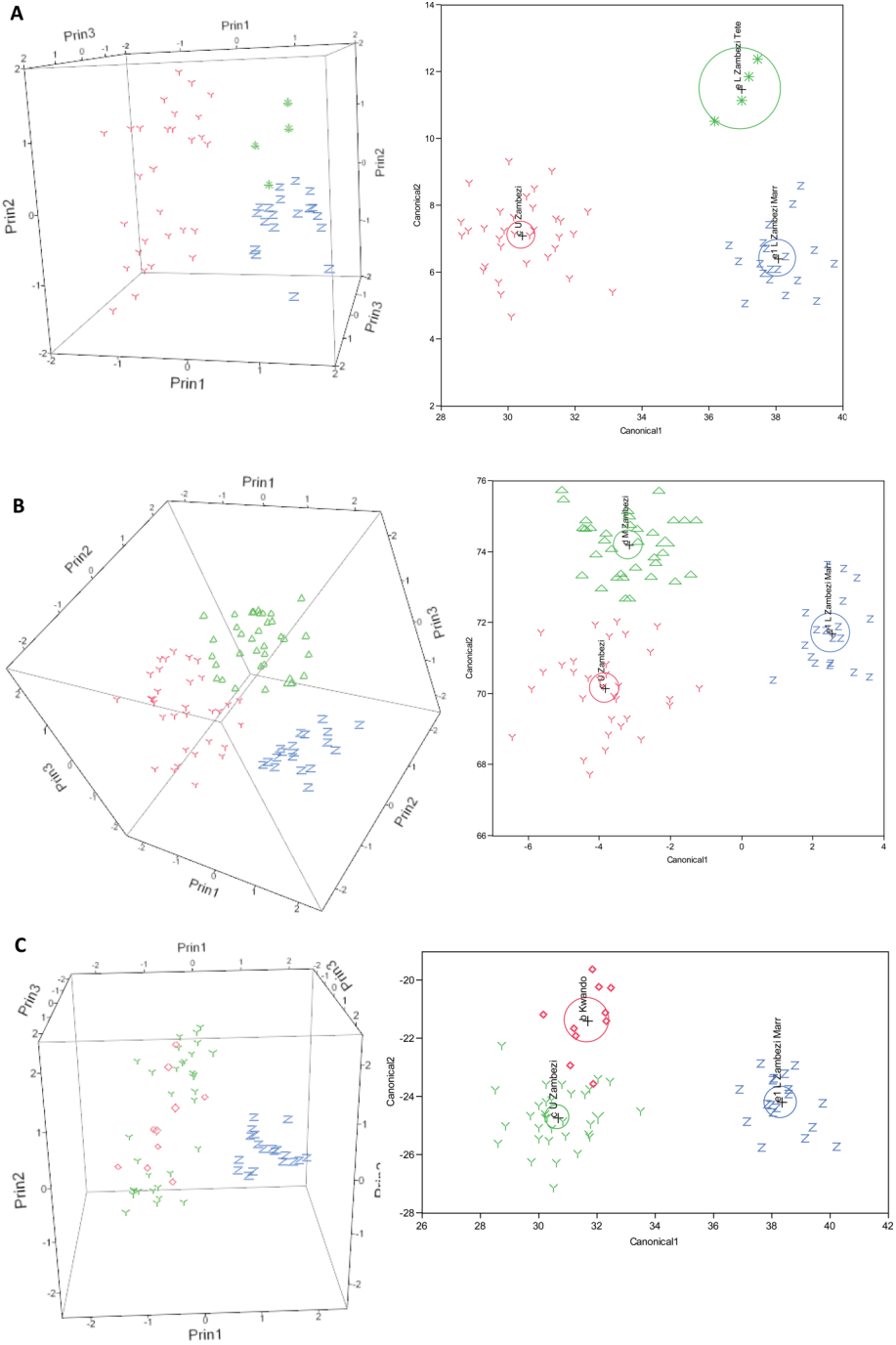
Very strong differentiation in terms of number of characters with significant differences was observed between Upper Zambezi and Middle Zambezi specimens (that is, direct neighbours, separated only vertically by about 100 m): nine characters at  $p < 0.01$  (Table 2). The differentiation between the very distant populations of the Upper and the Lower Zambezi was of similar strength: eight characters were significantly different at  $p < 0.01$  (as previously observed, Table 1). Weaker, but also marked, was the differentiation between Lower and Middle Zambezi specimens: six characters were significantly different at  $p < 0.01$ . The PCA confirmed differentiation among the three samples, as also seen in DFA (Figure 5B).

The Kwando sample was differentiated from the Lower Zambezi sample in nine characters ( $p < 0.01$ ), whereas compared with the Upper Zambezi sample this number was only one. PCA and DFA (Figure 5C) confirmed the association of the two samples from above the Victoria Falls versus that from the Lower Zambezi. The Upper Zambezi sample and that from the Kwando are therefore regarded as representing a continuous population.

The Okavango sample was well differentiated from the Lower Zambezi sample in eight characters ( $p < 0.011$ ). Between the Okavango and the Upper Zambezi samples, however, only BD/SL differed at  $p < 0.01$ , and – together with supportive evidence from PCA and DFA (Figure 5D) – we regard the Okavango samples, Kwando samples and Upper Zambezi samples as representing a continuous population with perhaps mild and subspecific, clinal differentiation.

We used PCA on correlations to test for differences in body shape on the whole data set (Figure 5E). PCA reduced redundancy in the data set successfully, as 57.9% of the variability was explained by the first three principal components alone (see Appendix, Table A2).

Principal component 1, P1, was loaded positively by LD, LA, nD (all “excellent”), CPD/CPL, nA (“very good”), BD/SL (“good”), pD/SL, LSo/HL (“fair”), and LPF/HL, LSc/HL (“poor”). P1 was negatively loaded by CPL/SL (“good”) and HL/SL (“fair”). It therefore seemed to represent a gradient for long unpaired fins carrying many rays, a deep but short caudal peduncle and a deep body (or vice versa). P2 was loaded positively by PDL/SL, HL/Na (“very good”), PAL/SL,



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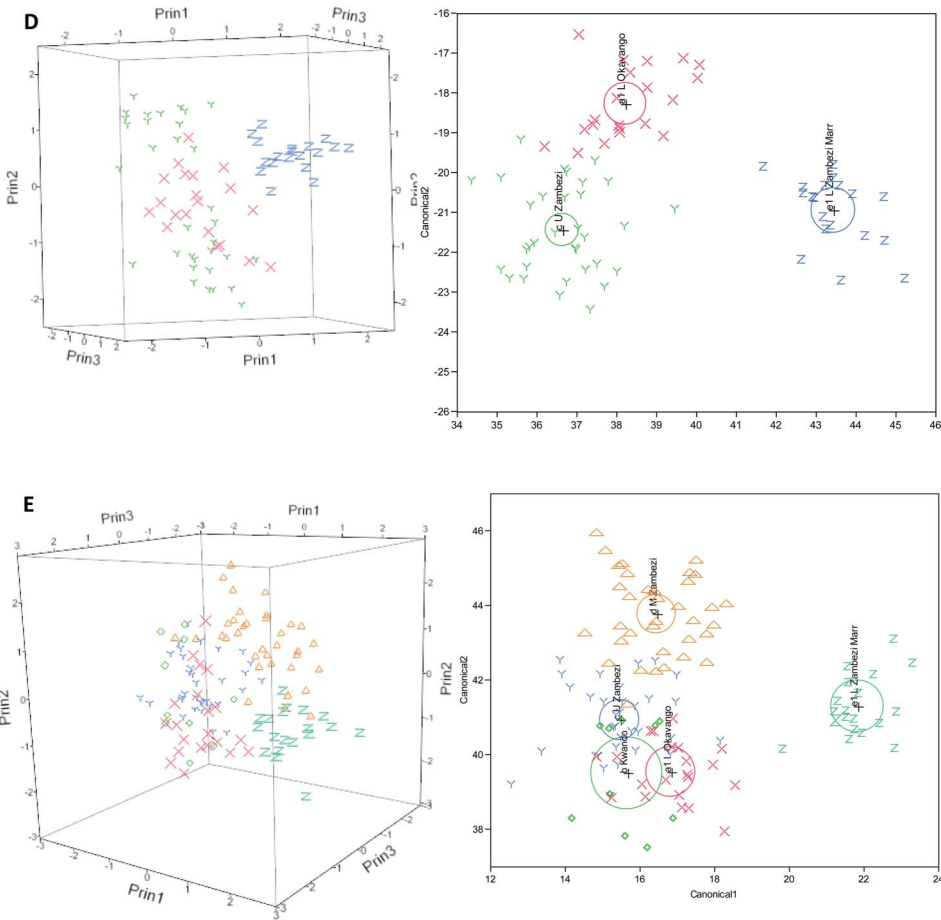


Figure 5. (A) Principal components analysis and discriminant function analysis on correlations for morphological characters in *Cyphomyrus discorhynchus* species complex. (A) Green stars, specimens from type locality, the Lower Zambezi at Tete ( $n = 4$ ); Blue Z symbols, from Lower Zambezi at Marromeu ( $n = 19$ ); red Y symbols, from Upper Zambezi ( $n = 33$ ). Data set included all 19 characters of Table A2. (B) Green triangles, specimens from Middle Zambezi (Batoka Gorge,  $n = 35$ ); blue Z symbols, from Lower Zambezi at Marromeu ( $n = 19$ ); red Y symbols, from Upper Zambezi ( $n = 36$ ). Data set included 15 rather than 19 characters, the non-separating characters (PAL/SL, LA/SL, pD/SL, CPL/SL) excluded by stepwise variable selection. (C) Red diamonds, specimens from Kwando River ( $n = 11$ ); blue Z symbols, from Lower Zambezi at Marromeu ( $n = 19$ ); green Y symbols, from Upper Zambezi ( $n = 36$ ). Data set included 18 rather than 19 characters (SPc excluded). (D) Red X symbols, specimens from Okavango River ( $n = 21$ ); blue Z symbols, from Lower Zambezi at Marromeu ( $n = 19$ ); green Y symbols, from Upper Zambezi ( $n = 36$ ). Data set included 17 rather than 19 characters (PAL/SL, PD/SL excluded). (E) Red X symbols, specimens from Okavango River ( $n = 21$ ); blue-green Z symbols, from Lower Zambezi at Marromeu ( $n = 19$ ); blue Y symbols, from Upper Zambezi ( $n = 33$ ); orange triangles, from Middle Zambezi ( $n = 35$ ); green diamonds, from Kwando River ( $n = 10$ ). Data set included all 19 characters of Table A2. [This figure can be viewed in colour online].

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PPF/SL (“good”), CPD/CPL, SLS (“poor”), and negatively loaded by OD/HL, CPL/SL (“good”), and pD/SL, LSo/HL (“fair”). P2 therefore represented a gradient for a long trunk, a deep but short caudal peduncle, wide nare separation but small eye. P3 was loaded positively by LSc/HL (“excellent”), LSo/HL, PAL/SL, LPF/HL (“fair”), PDL/SL (“poor”), and negatively loaded by HL/SL (“very good”), and nD, nA (“poor”). The gradient represented by P3 therefore was along a long snout and long underside of the trunk going together with a short head and fewer rays of the unpaired fins (or vice versa).

The samples from the Lower and Middle Zambezi were found at more positive values for P1 and P2 (namely Canonical 1 and 2 in terms of DFA) than the Upper Zambezi/Okavango samples (Figure 5E). Among the Lower and Middle Zambezi samples ( $n = 53$ ), only a single one from the Middle Zambezi was misclassified as an Upper Zambezi/Okavango system specimen (Kwando, actually) in DFA. Not a single specimen from the Okavango/Upper Zambezi system ( $n = 64$ ) was misclassified as a Lower/Middle Zambezi specimen.

The question arises whether or not there is an available species to which the Upper Zambezi/Okavango system form of Zambezi parrotfish can be attributed. The answer seems to be yes: it is *Marcusenius cubangoensis* Pellegrin, 1936 that was synonymized with *C. discorhynchus* (Peters, 1852) by Jubb (1967) and Jubb and Ghaiger (1971). *Marcusenius cubangoensis* originates from Angola, close to the erstwhile Vila da Ponte on the upper Cubango or Okavango (location 2 on Figure 2). *Marcusenius cubangoensis* has no notable anatomical differences to the Upper Zambezi/Okavango system samples of the present paper, but together with these differs markedly from the Middle and Lower Zambezi samples (see Appendix, Table A1).

The two samples (three specimens) from different locations on Lake Tanganyika differ substantially from each other but on the whole resemble closely *C. discorhynchus* (Peters, 1852). The Sumba specimens are outstanding in the highest CPD/CPL and PAL/SL values and maximum SLS count among all samples of the present study, whereas the Msamba sample is somewhat less extreme and even differs strongly from the Sumba specimens in its lower PAL/SL. These fish are definitely not the form found in the Upper Zambezi/Okavango system (see Appendix, Table A1).

### ***EOD comparisons***

Specimens from the Lower and Middle Zambezi all displayed EODs with four phases: in addition to the two strong main phases, P1 and N1, there were an initial head-negative phase N0 and a terminal head-positive P2 (illustrated in Figure 4). The EODs recorded from specimens from the Upper Zambezi had much weaker N0 and P2 phases (Figure 6). One Upper Zambezi specimen's EOD (excluded from the statistical analysis, below) did not show a P2 phase at all. The sample size of Middle and Lower Zambezi specimens was not sufficient for statistical tests (see Appendix, Table A3).

Specimens from the Kwando River showed somewhat stronger N0 and P2 amplitudes, and longer N0 duration but shorter P1 duration, than Upper Zambezi specimens (see Appendix, Table A3), and MANOVA/ANOVA analysis confirmed that the differences between the two Upper Zambezi populations were statistically significant (Table 3). Excepting N0dur, all duration and “area” measures were shortest (smaller) in Lower and Middle Zambezi specimens. The single type locality specimen's EOD

Table 2. MANOVA on morphology of members of *Cyphomyrus discorhynchus* species complex from the Zambezi, Kwando, and Okavango rivers.

	PDL/ SL	PAL/ SL	LD/ SL	LA/ SL	PPF/ SL	pD/ SL	CPL/ SL	CPD/ CPL	LSc/ HL	HL/ SL	BD/ SL	nD	nA	SPc	SLS
MANOVA	<b>0.0013</b>	<10 <sup>-4</sup>	<10 <sup>-4</sup>	<10 <sup>-4</sup>	<10 <sup>-4</sup>	<10 <sup>-4</sup>	<10 <sup>-4</sup>	10 <sup>-4</sup>	<10 <sup>-4</sup>	0.016	<10 <sup>-4</sup>	<10 <sup>-4</sup>	<10 <sup>-4</sup>	0.0212	<10 <sup>-4</sup>
ANOVA post tests <sup>1</sup>															
Okv,			<0.01												
Kwando															
Okv, UZ															
Okv, MZ			<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
Okv,			<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
LZ-Marr															
Kwando,			<0.01												
UZ															
Kwando,			<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
MZ															
Kwando,			<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
LZ-															
Marr															
UZ, MZ			<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
UZ,			<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
LZ-Marr															
MZ,	<0.01		<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
LZ-Marr															

MANOVA *P* value, same for Wilk's Lambda, Roy's Greatest Root, Hotelling Lawley Trace and Pillai Trace Tests;  $F_{\geq 15,106} \geq 7.183$ . Significant ANOVA,  $F_{4,117} \geq 3.182$ . For abbreviations of characters, see Material and methods.

<sup>1</sup>Games Howell test. Okv, Okavango River ( $n = 21$ ); Kwando River ( $n = 11$ ); UZ, Upper Zambezi River ( $n = 36$ ); MZ, Middle Zambezi River ( $n = 35$ ); LZ-Marr, Lower Zambezi River at Marrameu ( $n = 19$ ).

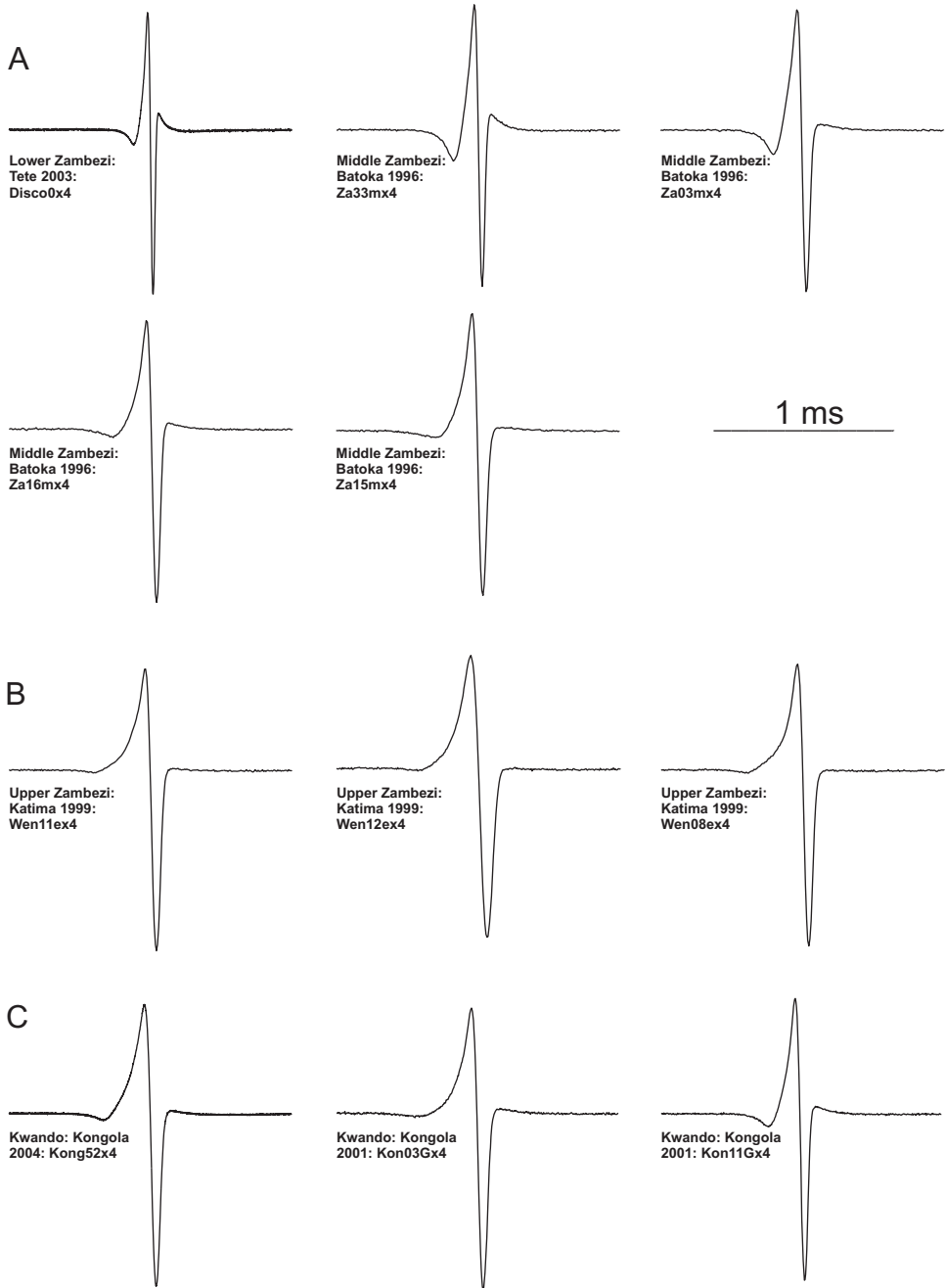


Figure 6. Electric Organ Discharge (EOD) pulse waveforms (Volts over time) for members of *Cyphomyrus discorhynchus* species complex. (A) EOD recorded from the single Lower Zambezi specimen (Tete) and from four Middle Zambezi specimens (Batoka Gorge). (B) Three specimens from the Upper Zambezi, Katima Mulilo. (C) Three specimens from the Kwando River, Kongola Bridge. Time-scale of 1 ms identical for all.

Table 3. Comparison of EOD characters between samples from the Upper Zambezi and Kwando. For abbreviations of characters, see Material and methods.

	N0amp (V)	N1amp (V)	P2amp (V)	N0dur (ms)	P1dur (ms)	N1dur (ms)	P1N1sep (ms)	P1area (V×ms)	N1area (V×ms)	PPF (Hz)
MANOVA										<0.0001
ANOVA	<0.0001		0.0039	<0.0001	0.001					

MANOVA *P* value, same for Wilk's Lambda, Roy's Greatest Root, Hotelling-Lawley Trace, and Pillai Trace, with  $F_{10,19} = 8.886$ . ANOVA *F* values, if significant,  $F_{1,28} \geq 9.875$ .

duration was a very short 128  $\mu$ s, for the Middle Zambezi specimens the value was  $243 \pm 11.9 \mu$ s (mean  $\pm$  SE); Upper Zambezi specimens,  $308.2 \pm 14.3 \mu$ s; Kwando specimens,  $283.8 \pm 11.5 \mu$ s. Amplitude spectra of Upper Zambezi and Kwando EODs peaked between 4.2 and 7.7 kHz, compared with between 4.2 and 8.8 kHz in the four Middle Zambezi specimens, and an exceptionally high 14 kHz in the single Lower Zambezi specimen (Figure 7). The single Lower Zambezi specimen's EOD also had the greatest bandwidth, with the -20-dB high-frequency cut-off at 48.3 kHz. Middle Zambezi and especially the Upper Zambezi specimen's EODs showed far less bandwidth, with the -20-dB cut-off frequency mostly not much beyond, or even below, 20 kHz. Spectra all showed a single peak, sometimes with a weak shoulder on the high-frequency side.

## Systematics

### Genus *Cyphomyrus* Myers 1960

#### *Diagnosis (from Myers 1960)*

Dorsal fin origin situated definitely anterior to anal fin origin. Dorsal fin with more rays than anal fin, and with its base longer than that of anal fin. Base of anal fin over half as long as base of dorsal fin. Mouth definitely inferior, or the chin with a short bulbous protuberance, which hides the essentially inferior position of the mouth. Teeth present only in the middle of the jaws, the median symphyial pair in the lower jaw not greatly enlarged. Body compact, deep, compressed, predorsal profile of back convex or humped. Origin of pelvic fins closer to base of pectoral fin than to origin of anal fin. Gill openings restricted, not extending below base of pelvic fin. Vertebrae 50 or fewer.

#### *Type species*

*Mormyrus psittacus* Boulenger, 1897 [current status *Cyphomyrus psittacus* (Boulenger, 1897)] by original designation of Myers (1960).

#### *Included species (valid unless otherwise stated)*

*budgetti*, *Marcusenius* Boulenger, 1904 [current status: junior synonym of *Cyphomyrus psittacus* see Bigorne 1990a: 314; Bigorne 1990b: 150]

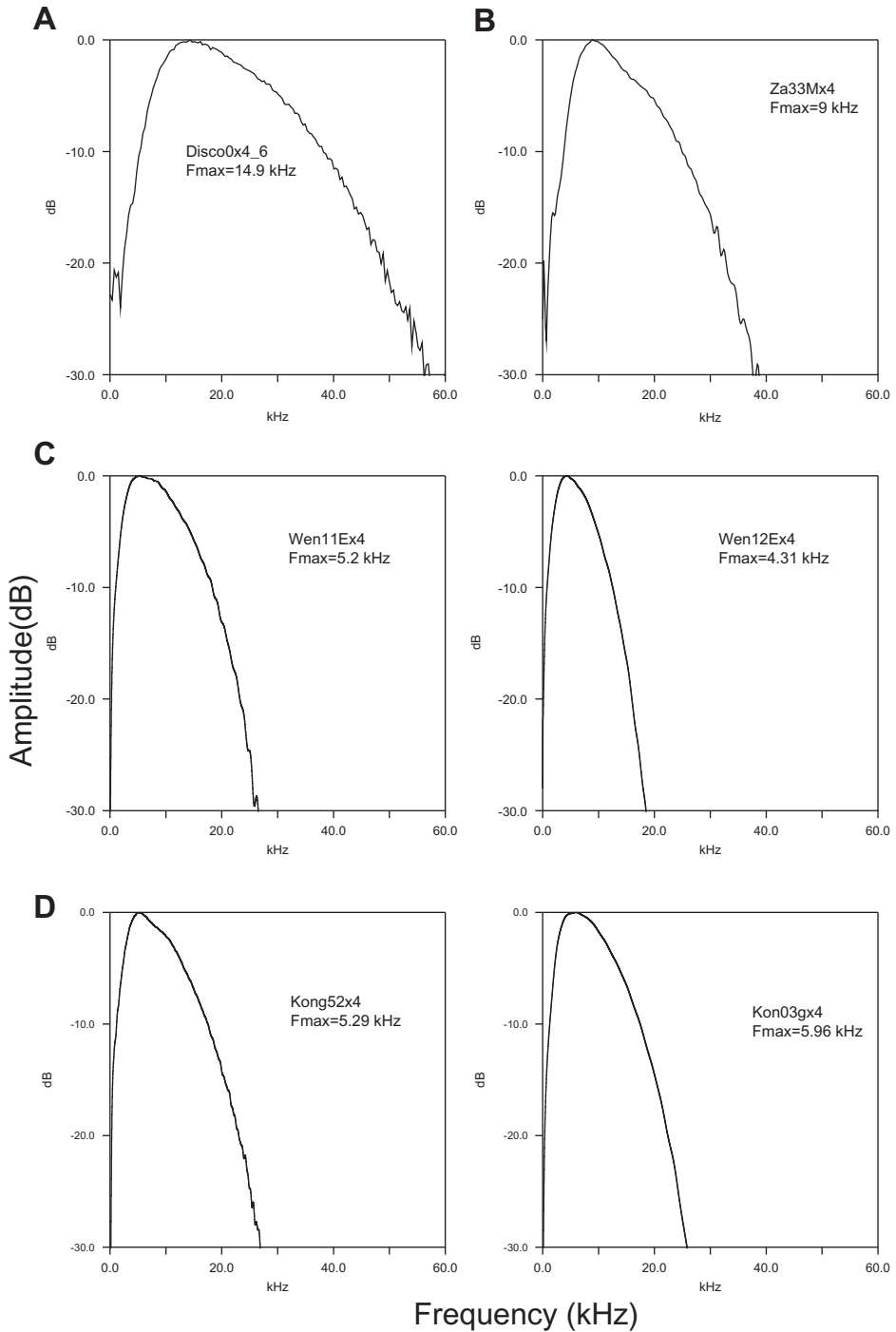


Figure 7. Amplitude spectra for members of *Cyphomyrus discorhynchus* species complex (amplitude in dB re: strongest signal component = 0 dB; abscissa: frequency in kHz). (A) spectrum for the Lower Zambezi specimen's Electric Organ Discharges (EOD); (B) for one of the Batoka Gorge specimens' EOD. (C) Two specimens' spectra from the Upper Zambezi, Katima Mulilo. (D) Two specimens' spectra from the Kwando River, Kongola Bridge.

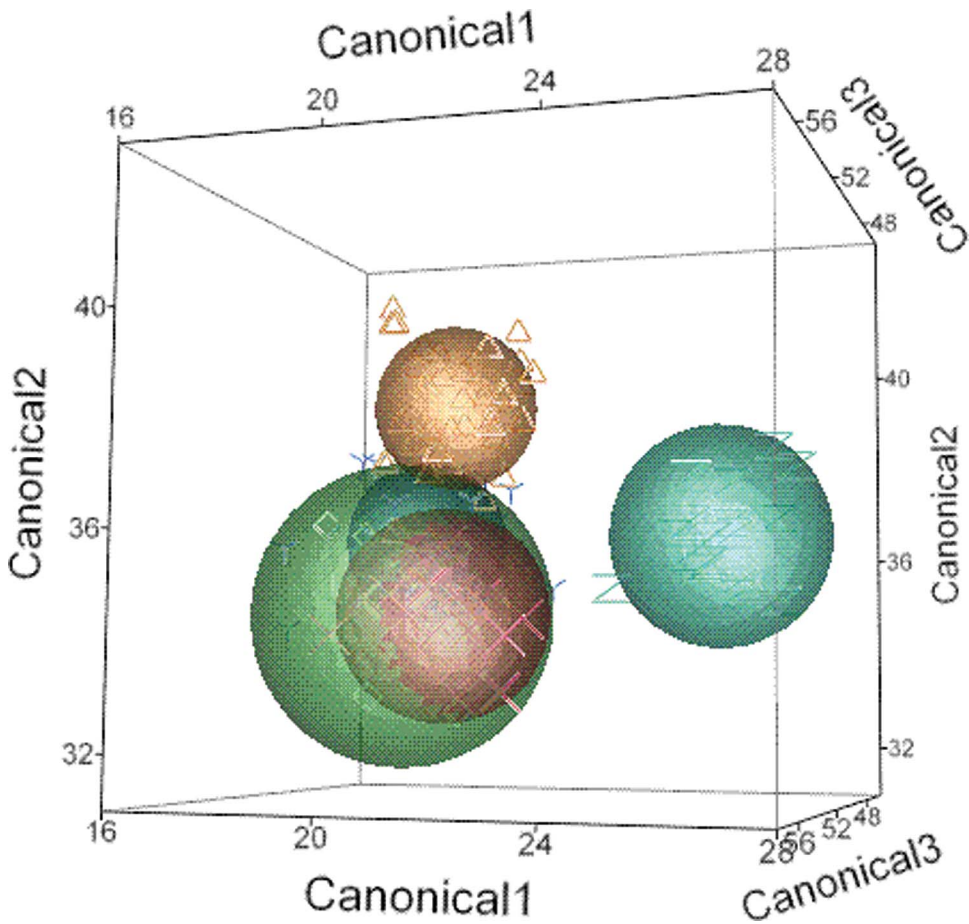


Figure 8. Canonical three-dimensional plot of discriminant function analysis on correlations for morphological characters in the *Cyphomyrus discorhynchus* species complex. Spheres show the 95% confidence region to contain true mean of group. Note spheres for the three populations of Okavango/Upper Zambezi system origin all together in the lower left; Lower/Middle Zambezi specimens shown as two separate spheres, suggestive of geographic differentiation (the sphere on the far right, and the uppermost sphere). Blue -green Z symbols, from Lower Zambezi at Marromeu ( $n = 19$ ); orange triangles, from Middle Zambezi ( $n = 35$ ); red X symbols, specimens from Okavango River ( $n = 21$ ); blue Y symbols, from upper Zambezi ( $n = 33$ ); green diamonds, from Kwando River ( $n = 10$ ). Data set included all 19 characters of Table B2. [This figure can be viewed in colour online.]

*discorhynchus*, *Mormyrus* Peters, 1852.

*cubangoensis*, *Marcusenius* Pellegrin, 1936 [current status: junior synonym of *Cyphomyrus discorhynchus* see Jubb 1967: 33; Jubb and Ghaiger 1971: 15]

*macrops*, *Marcusenius* Boulenger, 1909.

*psittacus*, *Mormyrus* Boulenger, 1897.

*wilverthi*, *Marcusenius* Boulenger, 1898.

*smithersi*, *Marcusenius* [current status: junior synonym of *C. discorhynchus* see Määr, 1962; Jubb 1967: 33]



*tanganicanus*, *Marcusenius* Boulenger, 1906 [current status: junior synonym of *C. discorhynchus* see Boulenger 1909: 81].

***Cyphomyrus discorhynchus*** (Peters, 1852)  
(Figure 1G)

Nominal species in boldface.

***Mormyrus discorhynchus*** Peters, 1852: 275.

*Petrocephalus discorhynchus*: Marcusen 1864: 150.

*Mormyrus (Petrocephalus) discorhynchus*: Sauvage 1880: 27.

*Marcusenius discorhynchus*: Boulenger 1898: 797.

*Cyphomyrus discorhynchus*: Myers 1960: 125, Van der Bank and Kramer 1996: 287; Skelton 2001: 97; Lavoué et al. 2003: 288; Kramer and Swartz 2010: 228, fig. 8.

*Hippopotamyrus discorhynchus*: Taverne 1971a: 104; Seegers 1996: 68.

***Marcusenius tanganicanus*** Boulenger, 1906: 455, pl. 30, fig. 1; Boulenger 1909: 81 (synonymy with *Mormyrus discorhynchus*).

***Marcusenius smithersi*** Määr, 1962.

*Cyphomyrus smithersi*: Jubb 1967: 33

*Hippopotamyrus smithersi*: Taverne 1971a: 104.

*Material examined*

See Material and methods section.

*Type specimens*. ZMB 3.674, lectotype. Paralectotypes: individuals ZMB 3.673, ZMB 3.675, ZMB 3.676. ZMB 23.374, one paralectotype plus remnants of a dissected specimen; all collected by W.C. Peters. Lectotype and paralectotypes designated by Seegers (1996: 69).

*Type locality*. “Mossambique”. In his 1868 publication, Peters specified that the origin of his specimens was “Tette” (present spelling Tete) on the Zambezi, and “the Licuare in Boror” (the Licuare is a short coastal river on the northern periphery of the Zambezi delta, discharging into the Indian Ocean at Quelimane; all Mozambique). Tete is below the Cahora Bassa dam, and separated from the Indian Ocean by 400 km.

*Diagnosis*

nD, median 33–34 (range 28–36); nA, median 24–25 (range 23–27); SPc, median 12 (range 12–13); SLS, median 64–69 (range 57–72); LD, mean 0.2977–0.3129 (range 0.2701–0.3239) of SL; LA, mean 0.2040–0.2124 (range 0.1844–0.2263) of SL; CPL, mean 0.2154–0.2215 (range 0.2066–0.2405) of SL; CPD, mean 0.2952–0.3002 (range 0.2657–0.3380) of CPL; BD, mean 0.2841–0.3530 (range 0.2464–0.3407) of SL; PDL, mean 0.5631–0.5779 (range 0.5455–0.6065) of SL; HL, mean, 0.2197–0.2373 (range 0.2168–0.2639) of SL. Bipolar EOD, of 130  $\mu$ s duration ( $n = 1$ ).

*Remarks*

Seegers (1996) gives a lively description of ecology and biology of specimens caught on or near Lake Rukwa.

For distinguishing between specimens of *C. discorhynchus* and *C. cubangoensis*, the most useful anatomical characters are: longer LD, longer LA, higher number of nD and nA, higher CPD/CPL in *C. discorhynchus* than *C. cubangoensis*.

***Cyphomyrus cubangoensis*** (Pellegrin, 1936) (resurrected species)  
(Figure 1A–E)

***Marcusenius cubangoensis*** Pellegrin, 1936: 48.

*Cyphomyrus cubangoensis*: Jubb 1967: 33; Jubb and Gaigher 1971: 15 (synonymy with *Cyphomyrus discorhynchus*).

*Hippopotamyrus cubangoensis*: Taverne 1971a: 104.

*Material examined*

See Material and methods section.

*Type specimens*

Syntypes: (8) MHNG 858.85 (1); MNHN 1936–0062 to 0064 (3), 1936-0065 (now 0); MRAC [ex MNHN 1936–65] (1); NMB 5216 (1).

*Type locality*

“Cubango: Dr. Monard”. Pellegrin (1936) gives in addition for all fish he studied that originated from the “Bassin du Cubango” (and not from the “Bassin du Congo”): “Les poissons ont été pris pour la plupart à Vila da Ponte ou dans ses environs immédiats, quelques uns à 120 Km. plus au sud mais toujours en territoire portugais, dans le Rio Mbalé, un petit affluent.” The present name of Vila da Ponte is Kuvango. The small town of Kuvango is located in the state/region of Huíla (Angola) at 14°27'11" S, 16°18'03" E.

*Diagnosis*

nD, median 30–31 (range 28–33); nA, median 22.5–23 (range 21–24); SPc, median 12 (range 10–12); SLS, median 65–66 (range 59–71); LD, mean 0.2613–0.2797 (range 0.2445–0.3001) of SL; LA, mean 0.1724–0.191 (range 0.1649–0.2086) of SL; CPL, mean 0.2311–0.2395 (range 0.1943–0.2532) of SL; CPD, mean 0.2596–0.2693 (range 0.2151–0.3299) of CPL; BD, mean 0.2713–0.2953 (range 0.2413–0.3388) of SL; PDL, mean 0.5686–0.5856 (range 0.5475–0.6071) of SL; HL, mean, 0.2251–0.2352 (range 0.2073–0.2697) of SL. Bipolar EOD, of 220–385  $\mu$ s duration.

*Description*

Head broadly rounded, lower jaw protruding less forward than upper, with inferior mouth and chin with a short bulbous protuberance. Deep body laterally compressed, with arched back. Long dorsal fin, median number of rays 30–31 (range 28–33), originating clearly in front of anal fin, median number of rays 22.5–23 (range 21–24). Dorsal and anal fins obliquely orientated with anterior portion higher than posterior portion. Usually dark band from dorsal to anal fin. Scales extending anteriorly

to operculum and pectoral fins. Caudal peduncle slender and subcylindrical over the entire length, usually slightly less than one-quarter of SL. Tail fin with broadly rounded lobes. EOD bipolar and tetraphasic, of 220–385  $\mu$ s duration (at 25°C and “5% threshold criterion”; explained in Material and methods).

*Colour in preservation*

In various shades from ochre to brown. Dark band from dorsal to anal fin usually fading with conservation time in alcohol.

*Ecology*

Adult specimens prefer larger river channels with soft bottom. Shoaling species. Small specimens also found in rocky environment.

*Behaviour*

Social, non-aggressive, at night very sensitive to light and shy during daytime (see Scheffel and Kramer 2000, 2006). Excellent aquarium species.

*Distribution*

Okavango River and delta whole length, Kwando River, Upper Zambezi.

*Relationships*

Close relatives are *C. discorhynchus* (Peters, 1852) as evidenced by the confusion of the two species, and *C. wilverthi* (Boulenger, 1898) and *C. psittacus* (Boulenger 1897), but none of the *Hippopotamyrus ansorgii* complex of species included in the genetic studies of Kramer et al. (2004), and Kramer and Swartz (2010: fig. 8).

*Etymology*

Pellegrin’s species name *cubangoensis* refers to the Okavango River where he sampled the type specimens.

*Remarks*

In Jubb 1967: 33 the synonymization of *C. cubangoensis* (Pellegrin, 1936) is presented as follows:

“*Cyphomyrus* Myers, 1960.

*Cyphomyrus discorhynchus* (Peters), 1852. Distribution: Zambezi River system, warm waters, and south along east coast to the Sabi River.

Synonyms: *Cyphomyrus cubangoensis* (Pellegrin), 1936. *C. smithersi* (Määr) 1962.”

No further comment is given.

For distinguishing between specimens of *C. discorhynchus* and *C. cubangoensis*, the most useful anatomical characters are: longer LD, longer LA, higher number of nD and nA, higher CPD/CPL in *C. discorhynchus* than *C. cubangoensis*.

## Discussion

Taverne (1971a) synonymized *Cyphomyrus* Myers, 1960 with *Hippopotamyus* Pappenheim, 1906 on the basis of detailed osteological studies that included *Hippopotamyus ansorgii* and several *Cyphomyrus* species, such as *discorhynchus*. He found that the two genera shared several features in the skeletal arrangement of the head and of the caudal skeleton: a well-developed lateral ethmoid, five circumorbital bones with the anterior orbital and the first infraorbital fused, the same form and arrangement of the bones of the snout and the lower jaw, five hypural bones of the caudal skeleton. He concluded that all of these species belonged “undisputably from an osteological viewpoint” (“sans doute possible, du point de vue de l’ostéologie”, Taverne 1971a; “indiscutablement”, Taverne 1971b) to the same genus, which was *Hippopotamyus* by priority. However, in neither publication was there a discussion of the characters underlying the significant differences in body shape between the *Cyphomyrus* and the *Hippopotamyus* groups of species that had been pointed out by Myers (1960), and an attempt to distinguish between plesiomorphic and apomorphic characters (that might decide the question) has not been made.

In none of five molecular-genetic studies has the genus *Hippopotamyus sensu* Taverne been recovered as monophyletic, instead, two independent lineages were observed (Van der Bank and Kramer 1996; Sullivan et al. 2000; Lavoué et al. 2003; Kramer et al. 2004; Kramer and Swartz 2010). This shows that *Hippopotamyus sensu* Taverne includes species that are not each other’s closest relatives among all other mormyrids. One of the two lineages was exclusively composed of *Cyphomyrus* species *sensu* Myers (1960). Although the type species for the genus *Hippopotamyus*, *H. castor*, has not yet been studied genetically, Lévêque and Bigorne (1985) have demonstrated morphologically its close affinity with *H. pictus*, a species that has been included in genetic studies. Lavoué et al. (2003) and Sullivan et al. (2000) confirmed the diphyly of the genus *Hippopotamyus* for *H. pictus* on one hand and *H. discorhynchus* and *H. wilverthi* on the other (the latter two species are termed *C. discorhynchus* and *C. wilverthi* in the present paper). Moreover, in southern African specimens the genetic distances between several *Hippopotamyus* as opposed to *Cyphomyrus* forms or species are so great that they are typical of generic differences. The sequence divergence of the mitochondrial cytochrome *b* gene has been determined as 7.8–11.4% between the two genera, which is similar to the genetic distance to *Marcusenius altisambesi* (9.5–12.0%) and almost as high as that to *Pollimyrus castelnaui* (11.9–13.3%). These values contrast with 2.4–4.0% sequence divergence among different *Hippopotamyus* species (Kramer and Swartz 2010). We therefore confirm our proposal to reinstate *Cyphomyrus* Myers, 1960 (Van der Bank and Kramer 1996). We believe a full understanding requires the revision of the genus *Hippopotamyus* that also includes the species from Angola, the Congo and from West and East Africa; however, this discussion is beyond the scope of the present paper.

We have observed considerable differentiation among *C. discorhynchus* specimens from the three sampling origins spanning the whole length of the Lower/Middle

Zambezi: (1) the Zambezi delta, (2) the type locality at Tete, and (3) the rapids region just below the Victoria Falls. Figure 8 shows the Lower and the Middle Zambezi samples as separate spheres, representing the 95% confidence region to contain true mean of group, in a three-dimensional canonical plot. On the basis of the statistical analyses described in Results, we believe the distinct separation of the two spheres represents subspecific, albeit substantial, geographic differentiation in the form of a cline, observed for the end points of the river section below the Victoria Falls, of 1400 km length and about 800 m difference in altitude. We do not follow Määr (1962) who described a new species, *Marcusenius smithersi*, from the Middle Zambezi (from a location that is now flooded by the Kariba Lake). The meristic data of *C. smithersi* are identical with the present samples from the Middle Zambezi, and some deviation among the measurements may be the result of either different measurement conventions, or the large size (280 mm) of the single specimen existing, the holotype (we could neither find out whether this still exists nor study it). Määr did not compare his specimen with samples from other origins, and the literature is not discussed.

We have also provided evidence that the Upper Zambezi/Okavango system holds a species different from *C. discorhynchus*, with the dividing line formed by the Victoria Falls. We are convinced that the species above the Victoria Falls has already been described as *Marcusenius cubangoensis* Pellegrin, 1936. Also in this part of the enormous river system (1300 km from Kuvango, the type locality, to Victoria Falls, passing by the Kwando/Chobe system), differentiation with geographical separation is present, even though in Figure 8 it appears as less marked compared with that observed for the Lower/Middle Zambezi system. We regard the geographical differentiation as non-dramatic and subspecific. Therefore, we resurrect *Marcusenius cubangoensis* Pellegrin, 1936 as *Cyphomyrus cubangoensis* (Pellegrin, 1936) for specimens from the Okavango/Upper Zambezi system.

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**Appendix A: Morphological and electrical differences between samples.**Table A1. Morphological measures for samples of the *Cyphomyrus discorhynchus* species complex from various origins. For abbreviation of morphological characters, see Material and methods.

L Zambezi (Type locality)		PDL/SL	PAL/SL	LD/SL	LA/SL	LPF/HL	PPF/SL	pD/SL	CPL/SL	CPD/CPL	LSO/HL	LSc/HL	OD/HL	HL/SL	HL/Na	BD/SL	nD	nA	SPc	SLS	SL (cm)
Mean/Median		0.5775	0.6051	0.3096	0.2124	0.9013	0.1845	0.4875	0.2154	0.2957	0.5259	0.4019	0.2384	0.2197	13.92	0.3230	33	25	12	64.5	12.8
Min		0.5656	0.6005	0.3044	0.2078	0.8138	0.1741	0.4797	0.2095	0.2792	0.5176	0.3944	0.2268	0.2168	12.95	0.3087	33	23	12	62	11.4
Max		0.5885	0.6095	0.3133	0.2201	0.9975	0.1952	0.4979	0.2223	0.3236	0.5366	0.4097	0.2458	0.2225	14.56	0.3407	35	25	12	67	13.3
SE/SIQ		0.0047	0.0018	0.0019	0.0027	0.0402	0.0048	0.0041	0.0031	0.0097	0.0043	0.0039	0.0041	0.0012	0.3463	0.0080	0.5	0.5	0	2	0.4
n		4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4
L Zambezi (Miarromeu)		0.5631	0.5976	0.3129	0.2113	0.9247	0.1845	0.4996	0.2215	0.3002	0.5283	0.3928	0.2707	0.2287	13.06	0.32	34	25	12	64	8.3
Mean/Median		0.5455	0.5723	0.2901	0.1960	0.8630	0.1741	0.4791	0.2068	0.2694	0.4995	0.3378	0.2409	0.2203	11.12	0.2955	32	23	12	57	6.6
Min		0.5845	0.6095	0.3310	0.2229	1.0216	0.1952	0.5161	0.2405	0.3261	0.5521	0.4158	0.2900	0.2548	14.7	0.3360	36	27	12	69	10.3
Max		0.0023	0.002	0.0027	0.0018	0.0087	0.0048	0.0022	0.0027	0.0032	0.0035	0.004	0.0033	0.0019	0.2368	0.0026	0.5	0.5	0	1.5	1.91
SE/SIQ		19	19	19	19	19	19	19	19	19	19	19	19	19	19	19	19	19	19	19	19
n		19	19	19	19	19	19	19	19	19	19	19	19	19	19	19	19	19	19	19	19
M Zambezi		0.5779	0.6058	0.2977	0.2040	0.9028	0.1795	0.4820	0.2175	0.2952	0.4736	0.3767	0.2364	0.2373	14.56	0.2841	34	24	12	69	11.9
Mean/Median		0.5488	0.5760	0.2701	0.1844	0.7676	0.1598	0.4537	0.2066	0.2657	0.4342	0.3431	0.2146	0.2169	11.82	0.2464	28	23	12	63	9.4
Min		0.6065	0.6316	0.3239	0.2263	1.0470	0.1957	0.5144	0.2299	0.3380	0.5523	0.4171	0.2571	0.2639	16.12	0.3163	36	26	13	72	14.4
Max		0.0024	0.002	0.0022	0.0020	0.0114	0.0014	0.0022	0.0010	0.0026	0.0047	0.0034	0.0022	0.0020	0.1543	0.0028	1.375	0.5	0	1.375	0.18
SE/SIQ		35	35	35	35	35	35	35	35	35	35	35	35	35	35	35	35	35	35	35	35
n		35	35	35	35	35	35	35	35	35	35	35	35	35	35	35	35	35	35	35	35
U Zambezi		0.5686	0.6024	0.2736	0.191	0.9018	0.1728	0.4802	0.2311	0.2693	0.4783	0.3762	0.2346	0.2352	13.73	0.2713	30	22.5	12	65	8.2
Mean/Median		0.5475	0.5740	0.2445	0.1649	0.7323	0.1572	0.456	0.1943	0.2151	0.4404	0.3235	0.1848	0.2073	11.29	0.2413	28	21	12	61	3.9
Min		0.5987	0.6423	0.2931	0.2086	1.0477	0.1867	0.5042	0.2526	0.3299	0.5222	0.4205	0.2757	0.2697	16.99	0.3003	33	24	12	71	12.9
Max		0.0021	0.0025	0.002	0.002	0.0152	0.0012	0.0017	0.0024	0.0044	0.0038	0.0044	0.0033	0.0033	0.25	0.0025	1	0.5	0	2	0.48
SE/SIQ		36	36	36	36	33	36	36	36	36	36	36	36	36	36	36	36	36	36	36	36
n		36	36	36	36	33	36	36	36	36	36	36	36	36	36	36	36	36	36	36	36
Kwando		0.5775	0.6023	0.2613	0.1880	0.8276	0.1780	0.4739	0.2376	0.2613	0.4946	0.3858	0.2403	0.2337	12.92	0.2909	30	23	12	65	8
Mean/Median		0.5525	0.5779	0.2453	0.1781	0.7662	0.1669	0.4593	0.2252	0.2228	0.4606	0.3557	0.2278	0.2103	10.79	0.2579	29	22	12	62	3.9
Min		0.6071	0.6280	0.2687	0.2086	0.9627	0.1932	0.4904	0.2532	0.2932	0.5287	0.4212	0.2609	0.2530	15.17	0.3204	31	24	12	71	11.1
Max		0.0061	0.0056	0.0024	0.0026	0.0178	0.0031	0.0032	0.0027	0.0077	0.0066	0.0063	0.0034	0.0048	0.4955	0.0057	0.5	0.375	0	1.375	0.84
SE/SIQ		11	11	11	11	10	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11
n		11	11	11	11	10	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11
Okavango		0.5732	0.6050	0.2797	0.1947	0.9107	0.1767	0.4876	0.2317	0.2596	0.5055	0.4039	0.2518	0.2251	12.12	0.2953	31	23	12	66	7.3
Mean/Median		0.5514	0.5868	0.2595	0.1762	0.8193	0.1544	0.472	0.2043	0.2311	0.4890	0.3814	0.2187	0.2111	10.28	0.2440	28	21	10	59	4.1
Min																					

(Continued)

Table A1. (Continued).

	PDL/ SL	PAL/ SL	LD/ SL	LA/ SL	LPF/ HL	PPF/ SL	pD/ SL	CPL/ SL	CPD/ CPL	LSo/ HL	LSc/ HL	OD/ HL	HL/ SL	HL/ Na	BD/ SL	nD	nA	SPc	SLS	SL (cm)	
Max	0.5985	0.6288	0.3001	0.2069	0.9845	0.2052	0.5111	0.2476	0.3246	0.5435	0.4209	0.2836	0.2383	15.4	0.3388	33	24	12	71	11.6	
SE/SIQ	0.0028	0.0024	0.0024	0.0016	0.0085	0.0028	0.0019	0.0021	0.0043	0.003	0.0024	0.0037	0.0013	0.27	0.006	0.5	0.5	0	1.5	0.55	
<i>n</i>	21	21	21	21	21	21	21	21	21	21	21	21	21	21	21	21	21	21	21	21	
Cubango																					
(Okavango <sup>1</sup> )																					
Mean/Median	0.5856	0.6101	0.2616	0.1724	0.9649	0.1807	0.4808	0.2395	0.2618	0.5228	0.4079	0.2844	0.2258	12.77	0.2809	30	23	12	66	7.9	
Min	0.5647	0.5960	0.2574	0.1690	0.9649	0.1807	0.4691	0.2310	0.2579	0.5175	0.3960	0.2844	0.2203	11.58	0.2759	28	22	12	66	7.6	
Max	0.5990	0.6237	0.2649	0.1774	0.9649	0.1807	0.4894	0.2453	0.2676	0.5283	0.4253	0.2844	0.2305	13.41	0.2880	31	23	12	66	8.4	
SE/SIQ	0.0106	0.008	0.0022	0.0026	—	—	0.0060	0.0043	0.0030	0.0031	0.0089	—	0.0030	0.5931	0.0036	1.125	0.375	0	—	0.25	
<i>n</i>	3	3	3	3	1	1	3	3	3	3	3	1	3	3	3	3	3	3	3	1	3
L Tang.	0.5847	0.6022	0.2902	0.2006	0.9122	0.1896	0.4846	0.2391	0.3070	0.5356	0.4132	0.2826	0.2125	15.13	0.2757	33	24	12	70	15	
Msamba																					
( <i>N</i> =1) <sup>2</sup>																					
L Tanganyika:																					
Sumba <sup>2</sup>																					
Mean/Median	0.5989	0.6429	0.2815	0.1947	0.8754	0.1788	0.4808	0.2316	0.3411	0.5183	0.3932	0.2730	0.2230	15.39	0.3030	32.5	24	12	71.5	12.7	
Min	0.5965	0.6379	0.2792	0.1943	0.8675	0.1780	0.4744	0.2257	0.3334	0.5180	0.3902	0.2629	0.2207	14.64	0.3027	31	23	12	71	12.7	
Max	0.6013	0.6479	0.2839	0.1951	0.8834	0.1795	0.4873	0.2375	0.3487	0.5186	0.3962	0.2830	0.2253	16.15	0.3033	34	25	12	72	12.8	
<i>n</i>	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	

Notes: SE, standard error; Median and SIQ (semi-interquartiles), for count measures (nD, nA, SPc, SLS). Localities, see Figure 2. L, M, U Zambezi: Lower, Middle and Upper Zambezi. L Tanganyika, Lake Tanganyika.<sup>1</sup> *Marcusenius cubangoensis* Pellegrin, 1936, type material.<sup>2</sup> *Marcusenius tanganyicanus* Boulenger, 1906, type material.

Table A2. Principal Components Analysis on correlations for 19 morphological characters of specimens of *Cyphomyrus discorhynchus* species complex from the Zambezi-Okavango-Kwando system. For abbreviations, see Material and methods.

Eigenvalue	4.8949	3.3995	2.7002	1.5246	1.023	0.8967	0.8463
Percent	25.763	17.892	14.211	8.024	5.384	4.719	4.454
Cum	25.763	43.655	57.866	65.89	71.275	75.994	80.448
Eigenvectors							
PDL/SL	-0.04844	0.35372	0.2042	0.25458	0.16832	0.05523	-0.02473
PAL/SL	-0.00184	0.33508	0.32918	0.22882	-0.11603	-0.02412	-0.13109
LD/SL	0.39818	0.02893	-0.16191	-0.01561	-0.10551	0.13777	0.14626
LA/SL	0.35959	0.03971	-0.05359	-0.19162	-0.12095	-0.02216	-0.07403
LPF/HL	0.20195	-0.11432	0.28752	-0.43523	-0.11736	0.05637	-0.12899
PPF/SL	0.03365	0.32533	0.21006	0.04861	0.238	0.22656	0.37019
pD/SL	0.24827	-0.25659	-0.17316	-0.00856	-0.16436	0.27366	0.40334
CPL/SL	-0.27304	-0.31896	-0.04681	-0.03105	0.13671	0.11147	0.26767
CPD/CPL	0.31647	0.244	-0.04028	0.04662	-0.21274	-0.27073	-0.08335
LSc/HL	0.18224	-0.14721	0.4324	0.00853	0.20096	-0.0544	-0.12841
LSo/HL	0.23172	-0.25588	0.3321	0.16332	0.14037	-0.1345	-0.07376
OD/HL	0.12051	-0.34104	-0.05187	0.28718	0.21699	0.07943	-0.17026
HL/SL	-0.18605	0.13214	-0.40643	0.32585	0.12232	-0.02533	-0.1265
HL/Na	0.0476	0.35275	-0.16449	-0.16294	-0.27836	0.06232	0.04133
BD/SL	0.25218	0.02943	0.14392	0.43134	-0.07254	0.06654	0.49431
nD	0.3421	0.00724	-0.27005	0.07877	0.15937	0.05971	-0.16051
nA	0.31815	0.01363	-0.2444	0.17702	0.27537	-0.01597	-0.25815
SPc	0.08489	0.10445	-0.11973	-0.27173	0.45617	-0.67156	0.38598
SLS	0.06461	0.23836	-0.01885	-0.33392	0.50682	0.52025	-0.07756
Component loadings							
PDL/SL	-0.10717	0.65218	0.33555	0.31434	0.17024	0.0523	-0.02275
PAL/SL	-0.00407	0.61781	0.54092	0.28253	-0.11736	-0.02284	-0.1206
LD/SL	0.88095	0.05334	-0.26606	-0.01927	-0.10672	0.13046	0.13455
LA/SL	0.79557	0.07322	-0.08806	-0.2366	-0.12233	-0.02098	-0.0681
LPF/HL	0.4468	-0.21078	0.47246	-0.5374	-0.1187	0.05338	-0.11866
PPF/SL	0.07445	0.59983	0.34518	0.06002	0.24072	0.21454	0.34055
pD/SL	0.54928	-0.47309	-0.28454	-0.01057	-0.16624	0.25914	0.37105
CPL/SL	-0.60409	-0.58809	-0.07692	-0.03834	0.13827	0.10556	0.24624
CPD/CPL	0.70017	0.44988	-0.06619	0.05756	-0.21517	-0.25637	-0.07668
LSc/HL	0.4032	-0.27142	0.71053	0.01053	0.20326	-0.05151	-0.11813
LSo/HL	0.51267	-0.47178	0.54572	0.20166	0.14198	-0.12736	-0.06786
OD/HL	0.26662	-0.6288	-0.08523	0.35459	0.21947	0.07522	-0.15663
HL/SL	-0.41162	0.24364	-0.66786	0.40234	0.12372	-0.02399	-0.11637
HL/Na	0.10531	0.65039	-0.27029	-0.20119	-0.28154	0.05901	0.03802
BD/SL	0.55793	0.05426	0.23649	0.5326	-0.07337	0.06301	0.45474
nD	0.75688	0.01335	-0.44375	0.09726	0.16119	0.05654	-0.14766
nA	0.70389	0.02513	-0.40161	0.21857	0.27852	-0.01512	-0.23748
SPc	0.18781	0.19258	-0.19674	-0.33552	0.46139	-0.63593	0.35508
SLS	0.14295	0.43948	-0.03097	-0.41231	0.51262	0.49265	-0.07135

*n* = 123 specimens. Middle Zambezi (*n* = 35), Upper Zambezi (*n* = 33), Kwando (*n* = 10); Okavango (*n* = 21), Lower Zambezi-Marromeu (*n* = 19), Lower Zambezi-Tete (*n* = 4), Cubango (*n* = 1).

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Table A3. Characters of the EOD pulse waveform of *Cyphomyrus discorhynchus* species complex from various origins. Amplitudes re: Plamp = 1 V. For abbreviations, see Material and methods.

	N0amp (V)	N1amp (V)	P2amp (V)	N0dur (ms)	P1dur (ms)	N1dur (ms)	P1N1sep (ms)	P1area (V× $\mu$ s)	N1area (V× $\mu$ s)	PPF (Hz)	EODdur (ms)	SL (cm)
L Zambezi ( <i>n</i> =1)	-0.1309	-1.405	0.14	0.0439	0.0422	0.0228	0.0195	0.0203	0.0186	13.96	0.1284	13.3
M Zambezi ( <i>n</i> =4)												
mean	-0.1472	-1.4	0.0648	0.0744	0.0866	0.0482	0.034	0.0389	0.0352	6.615	0.243	12.9
S.E.	0.0468	0.0745	0.0205	0.0084	0.0128	0.0054	0.0021	0.0037	0.0042	1.024	0.0119	0.64
minimum	-0.0559	-1.251	0.0324	0.0529	0.0589	0.0342	0.0287	0.0299	0.024	4.18	0.213	11.1
maximum	-0.2488	-1.603	0.1246	0.0909	0.1129	0.0604	0.0375	0.0469	0.0421	8.8	0.264	13.9
U Zambezi ( <i>n</i> =14)												
mean	-0.0297	-1.4901	0.0275	0.0348	0.157	0.0695	0.0437	0.0519	0.0491	5.4715	0.308	7.7
S.E.	0.0034	0.0229	0.0034	0.0028	0.0055	0.0041	0.0015	0.0014	0.0016	0.2019	0.0143	0.74
minimum	-0.0107	-1.34	0.006	0.0172	0.1158	0.0453	0.0356	0.042	0.0372	4.16	0.220	4.5
maximum	-0.0783	-1.686	0.06	0.0647	0.2070	0.1062	0.0582	0.0666	0.0657	7.69	0.386	13.3
Kwando ( <i>n</i> =10)												
mean	-0.0794	-1.513	0.0485	0.0583	0.1216	0.0614	0.0425	0.0505	0.0469	5.893	0.284	7.5
S.E.	0.0069	0.0569	0.0067	0.0033	0.0082	0.0048	0.0022	0.003	0.0028	0.318	0.0115	0.8
minimum	-0.0451	-1.114	0.0099	0.043	0.0837	0.0439	0.0325	0.0379	0.0342	4.59	0.224	4.2
maximum	-0.1128	-1.728	0.0743	0.0768	0.161	0.0908	0.056	0.065	0.0614	7.54	0.334	10.5