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A morphological study on species of African *Mormyrus* (Teleostei: Mormyridae) and their electric organ discharges

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Five species of *Mormyrus* Linné 1758, three from West Africa and one each from East and southern Africa, were compared morphologically, and their electric organ discharges (EODs) recorded in the field. The five species were morphologically well differentiated in terms of principal components analysis and discriminant analysis, with syntopical *M. rume* Valenciennes 1846 and *M. subundulatus* Roberts 1989 very close to but distinct from one another. Half the variation in the dataset was captured by PC1 alone, being mainly loaded by caudal peduncle depth and length, anal fin length, length of snout, pre-anal length, and dorsal fin ray count and length, in that order. Allopatric samples of *M. lacerda* Castelnau 1861 from the Upper Zambezi/Kwando system and Cunene River, Namibia, showed some differentiation regarded as infrasubspecific, similar to that of the *M. rume* samples from the Bandama River compared to those of the Comoé River, both in Côte d'Ivoire. The EODs, normalised to 25 °C, varied in average duration from 362 µs in the monopolar pulses of *M. tenuirostris* Peters 1882 sampled in Kenya, to 6 675 µs in the biphasic waveform pulses of *M. lacerda*, the waveform also displayed by all other *Mormyrus* species. The EOD of *M. hasselquistii* Valenciennes 1846 was so strong the fish was painful to handle. The EOD pulse duration of *M. rume* differed significantly between the sexes, being on average 1 334 µs (SE 106) in females and 2 008 µs (SE 195) in males.

Keywords: allopatric populations, body shape, intra-generic variation, intraspecific variation

Introduction

To the best of our knowledge, all the c. 200 known mormyrid fish species of Africa, including the *Mormyrus* species of the present study, possess electric organs for communication and electrolocation (reviews by Kramer 1990, Moller 1995, Kramer 1996, Bullock et al. 2005). These organs are located in the caudal peduncle, which ends in a forked tail fin that provides the main thrust for locomotion. The tail fin is operated by trunk muscles through tendons that pass through the electric organ, which does not itself carry mechanically functioning muscle cells, but is stiffened by Gemminger bones (Taverne 1971, 1972). Mormyrids are easily recognised in the field by their characteristic tail fin shape, and by their swimming mode reminiscent of pikes (and hence their German common name *Nilhechte*, Nile 'pikes').

Fishes of the genus *Mormyrus*, which comprises about 24 species, are distinguished from all other mormyrids by their long dorsal and short anal fins (Figure 1). *Mormyrus* species are relatively large fishes, and therefore of commercial interest. In southern Africa a *Mormyrus*, said to represent *M. longirostris* Peters 1852, has been identified in a rock painting near Lake McIlwaine (Chivero), Zimbabwe. Anglers have reported experiencing a mild electric shock when handling this species (Jubb 1967).

Mormyrus species prefer deep water, and are rarely caught in great numbers. A significant body of studies deals with their gonad condition, growth curves, age estimations, reproductive cycle, external morphology and feeding habits (for example, Iles 1960, Scott 1974, Gilmore 1979, van der Waal 1985, Adebisi 1987, Zaher et al. 1991, Kolding et al. 1992, Kouamélan et al. 1999, Fawole 2002, Authman and Khallaf 2009, Khallaf and Authman 2009, 2010). Successful reproduction in the laboratory was reported by Kirschbaum and Schugardt (2002). Modern taxonomic studies, including at least one *Mormyrus* species, are those of Taverne (1972), Lévêque and Bigorne (1985), van der Bank and Kramer (1996), Lavoué et al. (2000). The ethology of *Mormyrus rume* has been studied in the laboratory by Bauer and Kramer (1974), Kramer (1974, 1976), von der Emde (1992), von der Emde and Ringer (1992) and Walton and Moller (2010).

Many studies of the electric fish community relied on fish imported to Europe or America by tropical fish dealers, i.e. on fish of vague, one-word origin, such as 'Lagos', and of great taxonomical uncertainty. Field studies critically comparing populations are rare, and, with one exception, none linked morphological or genetic traits with electric organ discharge (EOD) characteristics. This is in contrast to Crawford and Hopkins (1989), who discovered a new species, *M. subundulatus* Roberts 1989, by comparing its EODs to those of the syntopical *M. rume* Valenciennes 1846 which has a similar EOD (see new species description by Roberts 1989).

The present report aims to characterise morphological and electrical differences among five *Mormyrus* species from selected locations in West, East and southern Africa

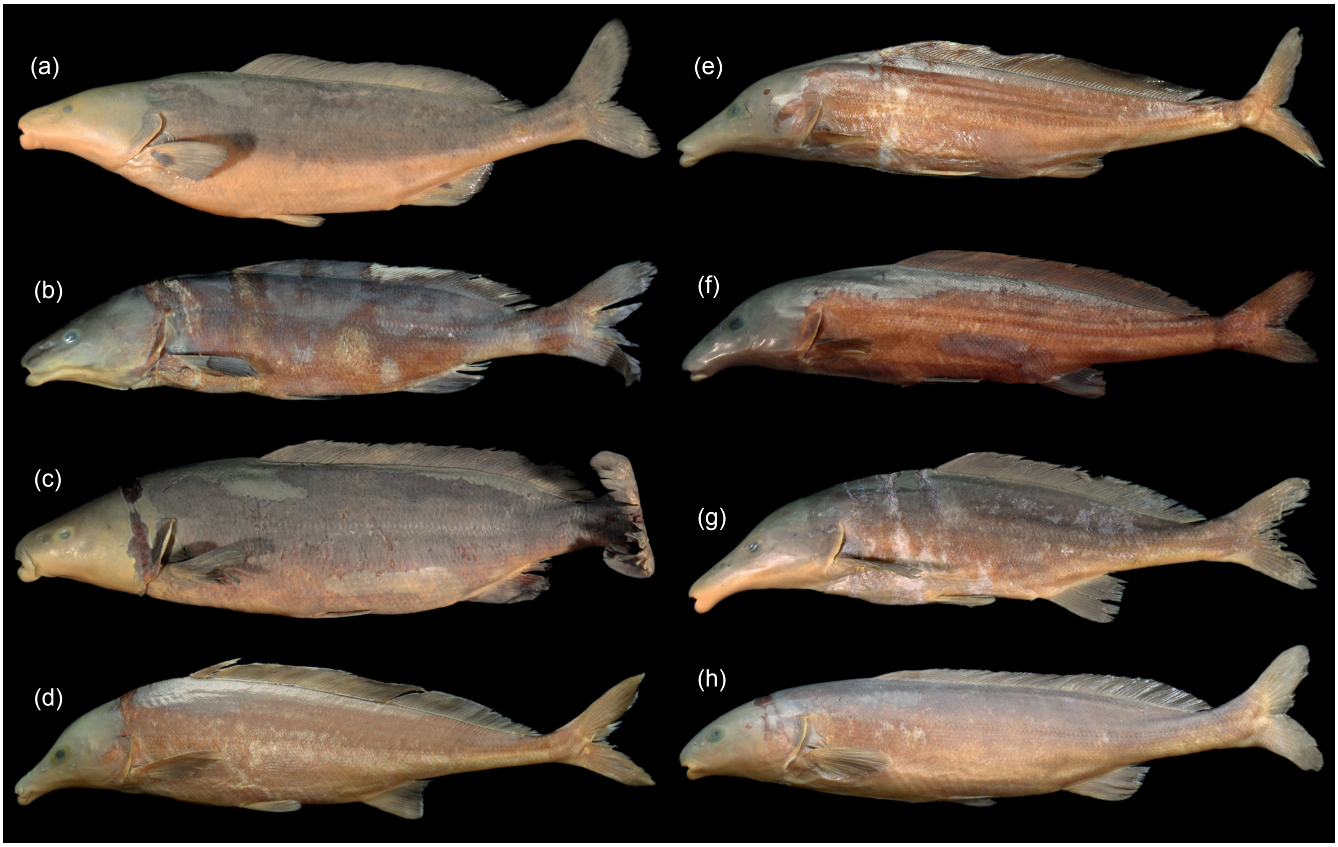

Figure 1: Photographs of the *Mormyrus* species studied: (a) *Mormyrus lacerda* from the Cunene River at Ruacana Falls, Namibia (ZSM 41770, field no. Ruac03); (b) *Mormyrus lacerda*, Upper Zambezi at Lisikili, Namibia (ZSM 41771, L11isi); (c) *Mormyrus lacerda*, Kwando River at Nkasa Island, Namibia (ZSM 41768, 5Fish); (d) *Mormyrus rume*, Comoé River at Kafolo, Côte d'Ivoire (ZSM 41788, Kaf117); (e) *Mormyrus rume*, Bandama River at Lamto, Côte d'Ivoire (ZSM 41790, Lam08); (f) *Mormyrus subundulatus*, Bandama River at Lamto, Côte d'Ivoire (ZSM 41777, LAM005); (g) *Mormyrus tenuirostris*, Tana River at Tana Primate Research Centre, Kenya (ZSM 41766, Ta19na); (h) *Mormyrus hasselquistii*, Comoé River at Kafolo, Côte d'Ivoire (ZSM 41783, Kaf116)

(Figure 2). Even though the specimens were collected over almost two decades, sample sizes from some of these locations are very limited. Nevertheless, it is considered that the results of this study add to the groundwork required for studies of the biogeography and diversity of African freshwater fish, such as that by Skelton (1994).

Material and methods

Morphology

The fish specimens examined were identified using dichotomous keys by Bell-Cross and Minshull (1988) and Skelton (2001), which are considered effective for fish populations occurring in southern Africa, and by Lévêque and Paugy (1984), Lévêque et al. (1990), Paugy et al. (2003) for West African populations.

Sixteen anatomical measurements (Figure 3) and counts of four meristic variables were performed on 56 specimens from various origins in Namibia, Botswana, Kenya and Côte d'Ivoire.

The following abbreviations were used:

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 peduncle
CPL = length of caudal peduncle (from end of anal fin base to midbase of caudal fin)
CPD = depth of caudal peduncle (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 centres of the pair of nares on one side
OD = eye diameter as defined by the orbital rims
LPF = length of the left pectoral fin
PPF = distance from the origin of the pelvic fin to the origin of the anal fin (for the more recent specimens)
SL = standard length (distance from the tip of the snout to the midbase of the caudal fin)

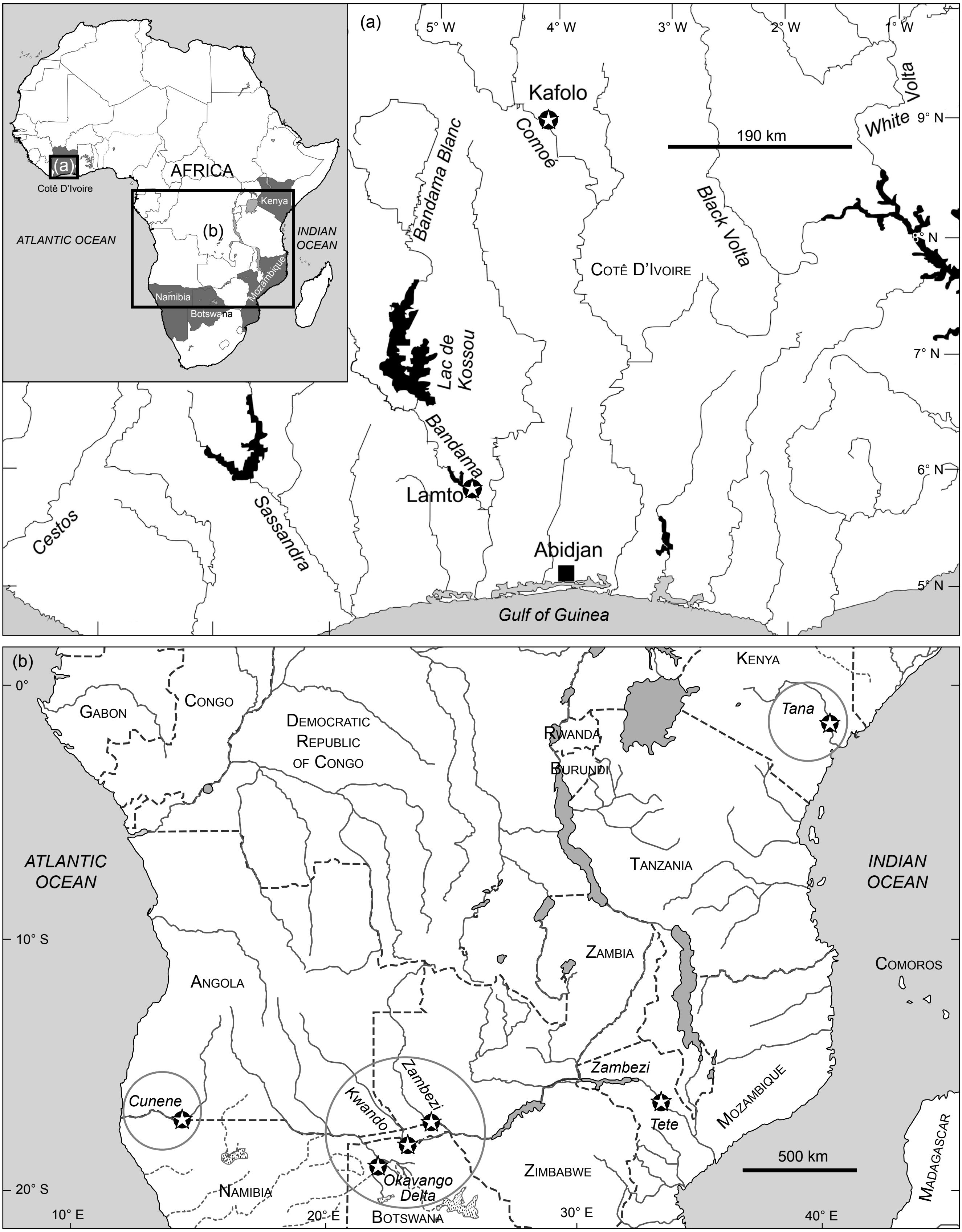

Figure 2: Maps of the collection sites for *Mormyrus* species used in this study: (a) West Africa with Côte d'Ivoire centred, showing locations Kafolo and Lamto; (b) East and southern Africa: the sampling locations on the Cunene River (Ruacana Falls, Namibia), Upper Zambezi/Okavango system (Namibia, Botswana) and Tana River (Kenya) are highlighted; Tete is located on the Lower Zambezi (Mozambique)

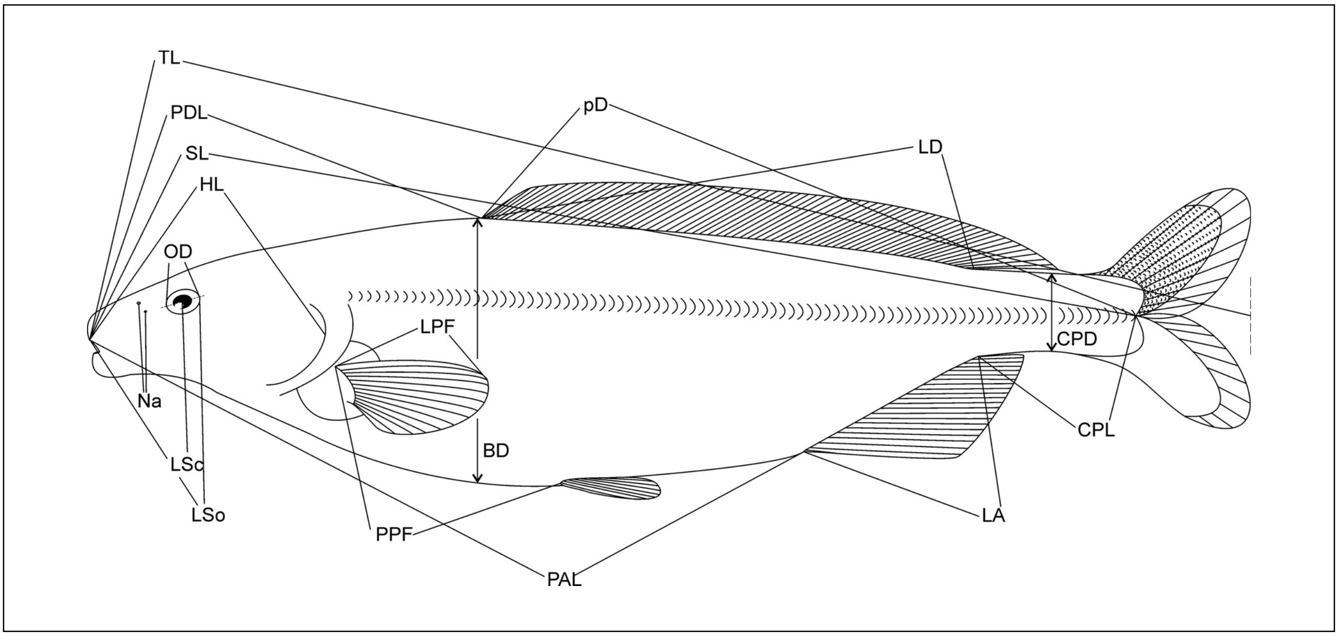

Figure 3: Morphological characters and their definitions. For abbreviations, see Material and methods

BD = body depth (the greatest vertical distance across the body)
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 by Skelton (2001: 67) (range of accuracy ±2 counts)

Abbreviations for the institutions and collections cited followed Leviton et al. (1985) and Fricke and Eschmeyer (2012). All measurements were made point-to-point. No projections into other planes were used. The gonads of *Mormyrus* specimens from Côte d'Ivoire were dissected for histological examination. Paraffin-embedded sections were stained following the Azan protocol (see Kramer 1997).

Electric organ discharges

Electric organ discharges (EODs) of live fish were recorded in the field immediately after capture, using the methods described in Kramer and Swartz (2010). Recordings were taken in a 37-litre plastic aquarium filled with water from the river from which a fish was collected. Conditions in the aquarium were kept constant throughout the analysis to exclude the possibility that water conductivity and temperature could affect EOD measurements.

Temperature (±0.1 °C) and water conductivity (±1 μS cm^{-1}) were constantly monitored using an electronic apparatus (LF318 Wissenschaftlich-Technische Werkstätten WTW, Germany). Fish were placed between a pair of carbon rod electrodes that were connected to a differential amplifier with a variable gain (up to ×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 (specified to at least 20 MHz at 8 bit vertical resolution and either 512, 2 048 or 4 000 points per sweep; but from 2002 onwards 100 MHz at 9 bit vertical resolution and 10 000 points per sweep). Data were numerically transferred onto disk via digital interface. Usually eight traces per fish were recorded. Except during the first year of the study, 1990, all the field equipment was battery-operated.

Custom-designed computer programs, programmed using a software package for signal analysis, Famos v6, were used for analysis of EODs. When necessary, EOD duration was normalised to 25 °C using a Q10 value of 1.5 (Kramer and Westby 1985) before data analysis.

Except in one species, the EOD waveform variables can be defined as follows (Figure 4):

- Namp: head-negative peak amplitude of N phase (measured from baseline to minimum, which was equal to −1 V by definition);
- P1amp: peak amplitude of positive P1 phase (re: Namp);
- P2amp: positive peak amplitude of post potential;
- Ndur, P1dur: durations of respective phases;
- P1Nsep: separation (or interval) between the peaks of the P1 and N phases;
- P1area, Narea: areas under the P1 and N phases; and
- EODdur: total EOD duration.

Durations in microseconds or milliseconds, as indicated; amplitudes in relative volts (re: N-phase amplitude = −1). Area-under-curve measures, dimension (V × microseconds). The start of the initial P1 phase and the end of the subsequent N phase were determined at a threshold level of + or −2% of Namp, respectively; P1 ended and N started at the zero-crossing between them. The reason why N ended at −2%, rather than at zero-crossing, was that the EODs of some specimens did not show an appreciable P2 phase, thus their return time to zero was extremely variable, and the value could not be determined due to noise.

A fast Fourier transform (FFT) routine provided by

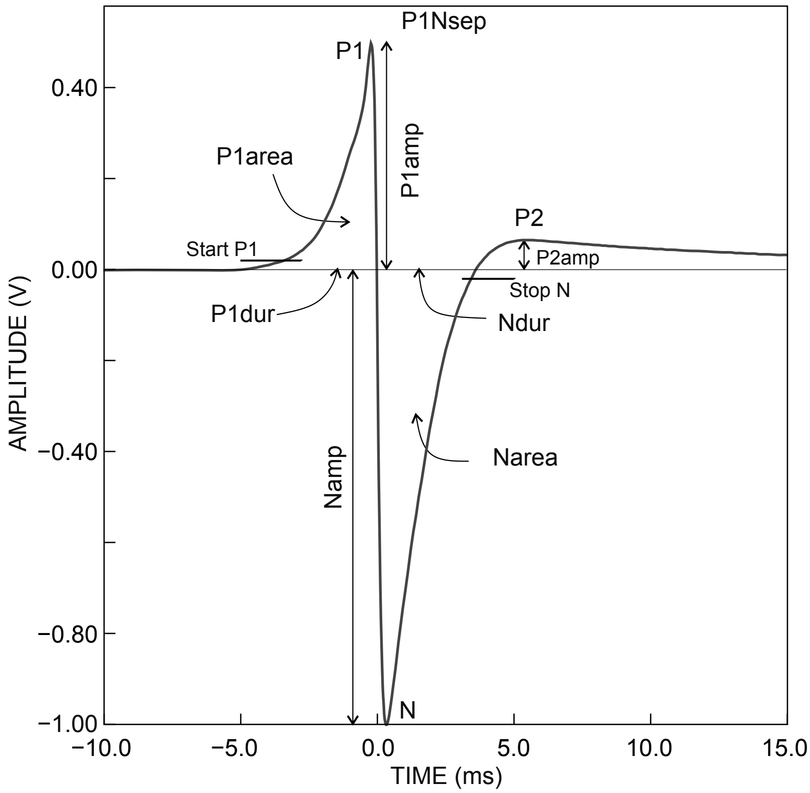

Figure 4: The common *Mormyrus* EOD type, present in all but the Kenyan sample of specimens, centred on the zero-crossing of the main transient, with baseline superimposed. Variables as used in the present study and their definitions. The beginning of an EOD was defined by 'start P1', at 2% of the absolute value of the amplitude of the N peak (or Namp that was −1 by definition). P1dur(ation) ended at time = 0 ms where the N phase started. An EOD (as well as Ndur) ended where the ascending slope of the N phase crossed the −2% threshold ('stop N'). This stop criterion was chosen because an appreciable P2 phase was not present in all *Mormyrus* specimens. P1Nsep, the interval between P1 peak and negative N peak. P1area and Narea, the areas under the P1 and N peaks, respectively. The EOD shown was recorded from a *Mormyrus lacerda* sampled from Guma/Okavango Delta. For the EOD waveform of *Mormyrus* specimens from Kenya, refer to Figure 7

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 FFT analysis was usually 2^{16}, 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 <1.3 Hz. The peak power frequency (PPF in Hz) was determined from these spectra.

Subsequent to EOD recording, fish were killed with an overdose of MS222 or 2-phenoxy-ethanol anaesthetic. Standard length (SL) was measured with Vernier callipers prior to fixing the specimen in 10% formalin for morphological studies.

Statistics

Univariate ANOVA and multivariate MANOVA were used to test for significant differences between samples. Means were given with ± standard errors, medians with ± semi-interquartiles. Principal component analyses (PCA) on correlations among anatomical characters were used to test differences in body shape among samples, because this does not require *a priori* assumptions about taxonomic groups. The component loadings, i.e. the principal component structure, were determined 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 recognised five levels of significance: loadings >0.32 or <−0.32 = poor, >0.45 or <−0.45 = fair, >0.55 or <−0.55 = good, >0.63 or <−0.63 = very good, and >0.71 or <−0.71 = excellent. These benchmarks accounted for 10%, 20%, 30%, 40% and 50% of the variance in the component, respectively. Discriminant analysis (DA) was used to find the best separation among the specimens from different origins in multidimensional space, using JMP v.9 software (SAS Institute, Cary, North Carolina, 2007). The best result was obtained by stepwise variable selection, as measured by the smallest −2LogLikelihood (i.e. minus two times the natural log of the likelihood function evaluated at the best-fit parameter estimates).

Material examined

Mormyrus lacerda Castelnau 1861

ZSM 41768 (3), field nos 5Fish (8 September 1993), 8Fish, 9Fish (9 September 1993), Namibia: East Caprivi: Kwando River: Nkasa Island in Mamili National Park, 18°26.5′ S, 23°38′ E, water: 108 µS cm^{-1} and 20 °C at 17:00, coll. FH van der Bank and B Kramer.

ZSM 41771 (3), field nos L03isi, L11isi, L21isi (5 March 1994); ZSM 41772 (4), L24isi, L25isi, L27isi, L34isi

(6 March 1994), Namibia: East Caprivi: Upper Zambezi River: Lisikili Lake, 17°33′ S, 24°29′ E, water: 56.1 μS cm^{-1} and 26.8 °C at 6:50, coll. FH van der Bank and B Kramer.

ZSM 41769, field no. 85, Namibia: East Caprivi: Upper Zambezi River: Kalimbeza fishing camp, 17°32′27.3″ S, 24°31′26.2″ E, 7 August 2004, water: 76.2 uS cm^{-1} and 18.9 °C at 07:00, coll. FH van der Bank and B Kramer.

ZSM 41770, field no. Ruac03, Namibia: Cunene River: just below Ruacana Falls, 17°24′24″ S, 14°13′01″ E, about 800 m altitude, 19 August 2006, water at 10:00: 45.8 μS cm^{-1} at 21.1 °C, coll. B Kramer and E Swartz.

Mormyrus tenuirostris Peters 1882
ZSM 41766 (4), field nos Ta19na (4 September 2001), Ta45na, Ta46na, Ta49na (6 September 2001), Kenya: Tana River: Tana Primate Research Reserve, 1°52′38.1″ S, 40°8′22.5″ E, approx. 48 m altitude, Tana River water at 17:00 on 2 Sept 2001: 185.6 μS cm^{-1} at 25.7 °C, coll. Luc De Vos and B Kramer.

Mormyrus rume Valenciennes 1846
Six specimens: ZSM 41785, field no. Kaf013 (17 April 1990, 25.9 °C, 104 μS cm^{-1}); ZSM 41786, Kaf020 (18 April 1990, 28.0 °C, 103 μS cm^{-1}); ZSM 41788 (4), Kaf055, Kaf105, Kaf108, Kaf117 (26 April 1990, 29.1 °C, 99 μS cm^{-1}); from Côte d'Ivoire: Comoé River: Kafolo (Campement de Recherche sur les Mouches Tsétsé), 9°36′ N, 4°19′ W, coll. B Kramer and M Postner.

Fifteen specimens: ZSM 41789 (4), field nos Lam57, Lam67, Lam67(A), Lamto102 (1 May 1990, 29.6 °C, 96 μS cm^{-1}); ZSM 41791, Lam017 (12 April 1991, 29.5 °C, 79.8 μS cm^{-1}); ZSM 41790, Lam08 (15 April 1991, 26.9 °C, 78.2 μS cm^{-1}); ZSM 41792 (2), Lam12, Lam24 (20 April 1991, 28.5 °C, 81.0 μS cm^{-1}); ZSM 41787 (2), Lam29, Lam30 (21 April 1991, 27.9 °C, 83.7 μS cm^{-1}); ZSM 41792 (2), Lam33, Lam34 (22 April 1991, 32.9 °C, 81.5 μS cm^{-1}); ZSM 41793 (3), Lam37, Lam38, Lam39 (22 April 1991, 32.9 °C, 81.5 μS cm^{-1}), Côte d'Ivoire: Bandama River: Station d'Écologie de Lamto, 6°11′ N, 5°0′ W, coll. B Kramer and I Kaunzinger.

Mormyrus hasselquistii Valenciennes 1846
Three specimens: ZSM 41784, field no. Kaf107 (16 April 1990, water 94 μS cm^{-1}, 26.4 °C); ZSM 41783 (2), Kaf026, Kaf116 (19 April 1990, water 26.1 °C, 110 μS cm^{-1}); Côte d'Ivoire: Comoé River: Kafolo Tsetse Research Station, 9°36′ N, 4°19′ W, coll. B Kramer and M Postner.

Mormyrus subundulatus Roberts 1989
Sixteen specimens: ZSM 41777 (3), field nos Lam001, Lam005, Lam013 (12 April 1991, 29.5 °C, 79.8 μS cm^{-1}); ZSM 41778, Lam07 (13 April 1991, 30.0 °C, 76.9 μS cm^{-1}); ZSM 41779 (2), Lam09, Lam10 (19 April 1991, 28.8 °C, 77.0 μS cm^{-1}); ZSM 41780 (5), Lam19, Lam23, Lam25, Lam26, Lam27 (20 April 1991, 28.5 °C, 81.0 μS cm^{-1}); ZSM 41781 (3), Lam28, Lam31, Lam32 (21 April 1991, 27.9 °C, 83.7 μS cm^{-1}); ZSM 41782 (2), Lam35, Lam36 (22 April 1991, 32.9 °C, 81.5 μS cm^{-1}); Côte d'Ivoire: Bandama River: Station d'Écologie de Lamto, 6°11′ N, 5°0′ W, coll. B Kramer and I Kaunzinger.

Results

Anatomical comparisons

The morphological characteristics of the West African *Mormyrus* species (Appendix 1) were used to determine the species, following the key by Bigorne (2003). The number of dorsal fin rays (median nD = 65, range 60–70), in the *M. subundulatus* sample neither overlapped that of the Bandama River *M. rume* sample (median nD = 83, range 72–87) nor of the Comoé River *M. rume* sample (median nD = 84, range 83–89). Also, the counts of the scales in lateral series, SLS, were in almost perfect agreement with the key (see Appendix 1 for comparisons). As expected from the key, the median SLS counts were higher in the two *M. rume* samples (median SLS counts of 105 and 101.5, respectively) than in *M. subundulatus* (median SLS = 88.5, range 87–92), with a single *M. rume* specimen from the Comoé River also showing only 92 scales, which was the maximum count recorded in *M. subundulatus*. The fin ray and scale count data of the key clearly distinguished between the two species *M. rume* and *M. subundulatus*. Among the measurements summarised by Bigorne (2003), LD/SL and HL/SL are in agreement with the present two samples of *M. rume* and *M. subundulatus*, respectively, whereas minimum LA/SL values in the Bandama sample of *M. rume* were still smaller than the minimum values of the key, though not so in the Comoé sample. These slight deviations from the summary given in Bigorne (2003) seem to show that the full extent of variation has not yet been determined in these two *Mormyrus* species from West Africa and Chad. As noted by Roberts (1989), and confirmed in the present sample, the caudal peduncle of *M. subundulatus* is deeper than that of *M. rume*, whilst a local fisherman had reported that only the former species (which Roberts subsequently recognised as the new species *M. subundulatus*) gave an electrical shock.

A characteristic trait of *M. hasselquistii* Valenciennes 1846 listed in the key and also present in our specimens, is that its dorsal fin begins far in advance of the pelvic fins. In combination with the position of the pelvic fins relative to the dorsal fin, the count of the circumcaudal peduncle scales (key range 26–34; range in our specimens 28–30) distinguished *M. hasselquistii* with certainty. Additional support for this were the dorsal and anal fin ray counts (nD and nA), the count of the scales in lateral series (SLS) and the measurements of LD/SL, LA/SL and BD/SL, which were all in agreement with the data of Bigorne (2003). OD/HL values in our sample overlapped, and extended to values greater than, the range given in Bigorne (2003). It should be noted that the manner in which this character is measured may vary among laboratories — i.e. point-to-point, as in the present paper, or, for example, by projection into a parasagittal plane and following right angles in certain, but not all, characters — and that the number of specimens per species as summarised by Bigorne (2003) is not given, but appears to be small in certain species (see Lévêque and Bigorne 1985).

The *M. lacerda* Castelnau 1861 specimens were identified according to Skelton (2001). The count data for nD, nA and SLS in this reference work corresponded to our samples' counts in *M. lacerda*, with the exceptions of the Upper Zambezi sample, which had up to 21 anal fin rays, and the Kwando sample, which had up to 20, rather than a maximum of 19, as given by Skelton (2001). As there has been no comparison of allopatric populations of *M. lacerda* to date, these range extensions are to be expected.

The East African *M. tenuirostris* Peters 1882 was identified by the late L De Vos (personal communication). The present specimens sampled in the Tana River, Kenya, agreed with the original description by Peters (1882) of one specimen of 125 mm length from the Athi River, Kenya. Whereas Copley (1941) did not list *M. tenuirostris*, Copley (1958) confirmed its presence in the Athi River. Whitehead (1959) cautiously confirmed the presence of '*Mormyrus* sp.' in the Tana River. Probably the first reference confirming the presence of *M. tenuirostris* in the Tana River was Seegers et al. (2003). Referring to the Kenyan ichthyofauna in general, these authors stated that 'the taxonomy of the genus *Mormyrus* is largely unresolved and tentative' (p 18). This call for caution evidently refers to *Mormyrus bernhardi* Pellegrin 1926, *Mormyrus hildebrandti* Peters 1882, and *Mormyrus kannume* Forsskål 1775, and concerns their validity or distribution within Kenyan freshwaters, but it does not cast doubt upon the validity of *M. tenuirostris* or its occurrence in the Tana River (p 29).

The first question of the present study was whether samples of *M. lacerda* from the Upper Zambezi, Kwando and Cunene rivers in southern Africa were differentiated from each other when compared to a distant relative, such as *M. rume* from the Bandama River, West Africa. Using principal components analysis (PCA), the three southern African samples of *M. lacerda* formed a close cluster that was well separated from *M. rume*. The three Kwando and the single Cunene specimens were close to, but a little outside the Upper Zambezi group. This was confirmed by discriminant analysis and, pending closer study using more individuals, this is considered evidence for intraspecific geographic variation in *M. lacerda* (Figure 5).

In a similar analysis including all samples studied, the *M. lacerda* specimens from the Upper Zambezi system, including the Kwando, were well differentiated from all other groups. The same held true for *M. hasselquistii* and *M. tenuirostris*, two species that are easily recognised both in the field and as collection specimens. This is in contrast to *M. rume* and *M. subundulatus*, which formed two clusters very close to, but distinct from, one another (non-overlapping 95% confidence limits to contain true mean of group; Figure 6), reflecting the great morphological similarity between these two species. The *M. rume* samples from the Bandama and the Comoé rivers were close together with some overlap of confidence limits, and thus the differentiation is regarded as infrasubspecific (Figure 6).

A PCA on all samples successfully reduced the redundancy: 76.6% of the variation in the dataset was explained by the first three components (Appendix 2). PC1 was positively loaded by CPL, LSc, LSo, nD and SLS (all 'excellent'), LD ('very good'), and pD ('good'); it was negatively loaded by CPD/CPL, LA, PAL, PPF (all 'excellent'), BD ('very good'), and PDL ('good'). Thus PC1 is a complex gradient, first of all for a caudal peduncle that is deeper the shorter it is (or *vice versa*: the less deep the longer), exemplified by *M. lacerda* with the shortest caudal peduncle but the highest score for CPD/CPL, as opposed to *M. rume* with the least deep but relatively longest caudal peduncle among the present samples (Appendix 1). PC1 also represents a shorter anal fin together with more rays in, and an increased length of, the dorsal fin (and *vice versa*); a greater number of scales in the lateral series together with a reduced PAL, reduced PPF, longer snout and decrease in body depth (and *vice versa*). PC2 is loaded positively by LPF ('excellent'), pD, PPF and LD ('good'), and negatively loaded by HL and PDL (both 'very good'). Thus PC2 is a gradient for a shorter head length and PDL (the predorsal section of the fish) going together with a longer pD and LD (rear section of the fish), but also longer PPF (and *vice versa*). *Mormyrus tenuirostris* from Kenya exhibited the longest head and PDL, and *M. hasselquistii* the shortest. Several characters loaded strongly on both PC1 and PC2, such as PDL, LD, PPF and pD. Only a single character loaded strongly, and negatively, on PC3: SPc ('very good'). In the present sample, the range of SPc scales spans a median of from 20 in *M. lacerda* and *M. subundulatus* to 30 in *M. hasselquistii.*

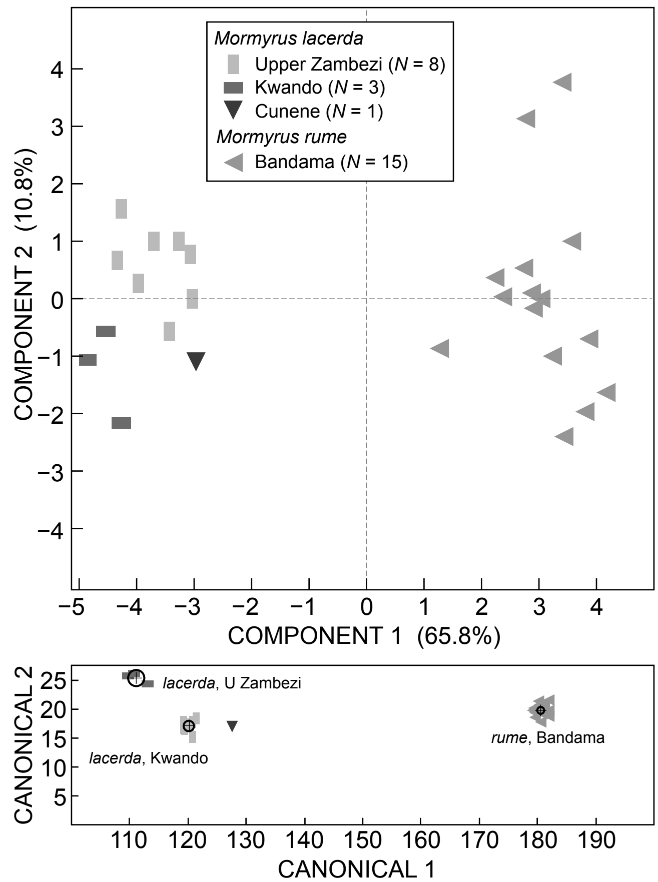

Figure 5: Principal components analysis (upper graph) and discriminant analysis (DA; lower graph) on the morphology of *Mormyrus lacerda* from three localities in southern Africa and of *M. rume* from Bandama. The single sample from Cunene was excluded from the DA analysis but its position on the graph is shown. Circles in DA graph = 95% confidence limit to contain true mean of group (group mean indicated by + symbol). Based on all 19 available characters

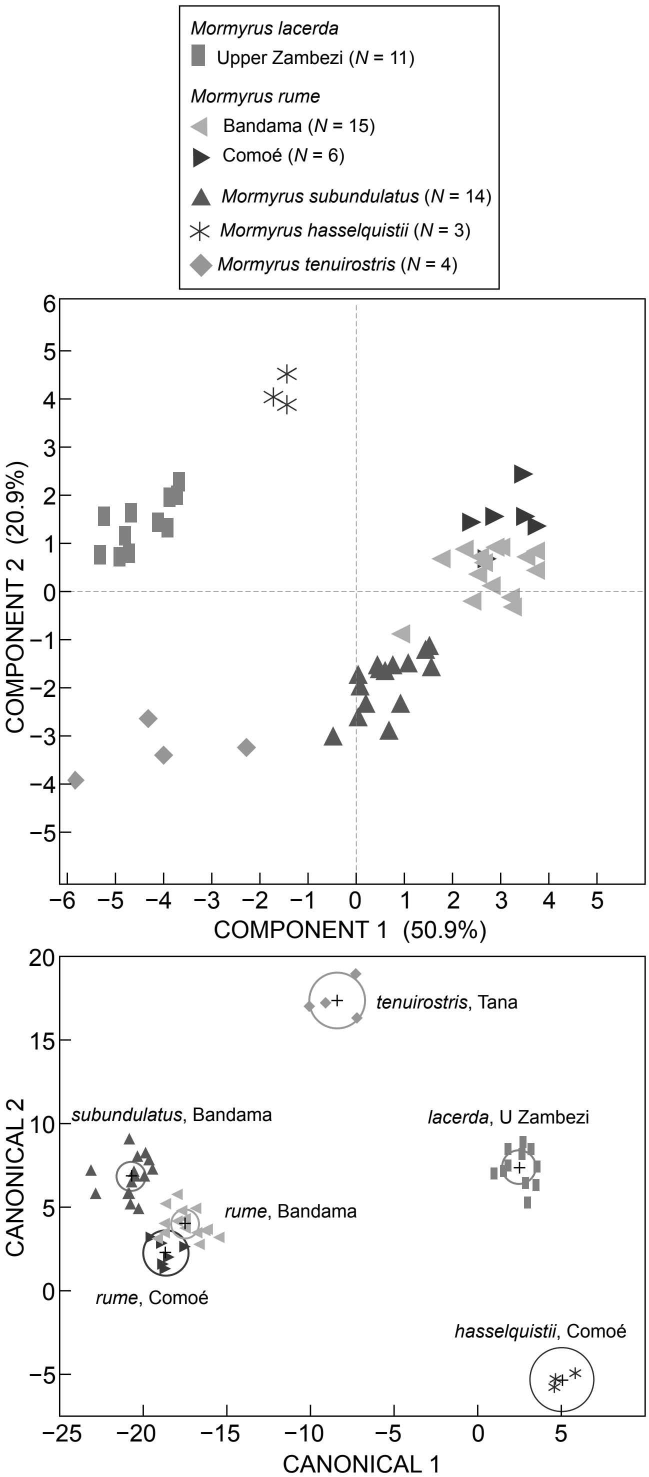

Figure 6: Principal components analysis and discriminant analysis on morphology of *Mormyrus lacerda* (Upper Zambezi system); *M. rume* (Bandama River and Comoé River); and *M. subundulatus*, *M. hasselquistii* and *M. tenuirostris*. Based on 18 characters, i.e. all except OD/HL, which did not contribute to discrimination

EOD comparisons

All but one *Mormyrus* species displayed an essentially similar, biphasic EOD waveform that varied in pulse duration among species. However, for the exceptional *M. tenuirostris*, see below. An EOD started with a head-positive (P1) phase that was followed by a head-negative main potential (N phase) and, in most cases, was terminated by a weak head-positive P2 phase of long duration that approached the baseline asymptotically (Figure 7). Using a 2%-amplitude criterion for the beginning and end of an EOD (see Material and methods, Figure 4), the EOD of *M. subundulatus* from Côte d'Ivoire was the shortest (mean 1 232 ± 61.3 µs, N = 16), and that of *M. lacerda* from the Upper Zambezi River, Namibia, the longest (6 675 ± 285 µs, N = 8) (disregarding the weak P2 phase of usually long duration; Appendix 3). In morphology as in EOD waveform, the pair of species which most closely resembled one another was *M. rume* and *M. subundulatus*, both being from the Bandama River, Côte d'Ivoire. The EOD of *M. rume* was longer (1 555 ± 118 µs) than that of *M. subundulatus* (1 232 ± 61 µs) from the same river, and the difference was significant (unpaired t-test, t = 2.56, N_1 = 16, N_2 = 11, p = 0.0164). This was in contrast to Crawford and Hopkins' (1989) findings whose EOD duration values for the two species were shorter (average 966 µs for *M. rume*, and 961 µs for *M. subundulatus*) than those in the present study, and did not differ significantly from each other. As already seen by Crawford and Hopkins (1989), and confirmed in the present study, the P1 phase amplitude was stronger in *M. rume* than in *M. subundulatus* and did not have a notable inflection point. Also, the rising slope of the N phase usually followed a more markedly sigmoidal course in *M. subundulatus* than in *M. rume*.

The present study found the P1 amplitude in *M. subundulatus* (mean amplitude 0.316, range 0.242–0.419) to be twice as strong as that reported by Crawford and Hopkins (1989) (mean 0.144, range 0.113–0.203), and hence more similar to that of *M. rume*. The difference between the two studies is explained in part by a difference in the size of the *M. subundulatus* specimens used: SL 22.5 cm (SD 1.2, N = 16) in the present study vs 8.48 cm (SD 4, N = 5) in the other study. The P1 amplitude of the present sample grew significantly with SL ($y = 0.005x + 0.195$; r^2 = 0.320, F = 6.591, p = 0.0224, N = 16). Hence, the expected P1 amplitude for an SL of 8.48 cm would be about 0.24, rather than 0.144. However, a dependency of P1 amplitude on SL in *M. rume* could not be demonstrated. The two studies agree in that *M. rume*'s P1 amplitude was significantly stronger than that of the syntopical *M. subundulatus* (unpaired t-test, t = 5.256, N_1 = 16, N_2 = 13, p < 0.0001).

The EOD of *M. hasselquistii* resembled that of *M. lacerda* in waveform and duration (which was 5 283 ± 73.5 µs, N = 3, Appendix 3, Figure 7). *Mormyrus hasselquistii* was unique in its strong pulse amplitude, subjectively much stronger than that of at least two *Mormyrus* species, *M. longirostris* (Jubb 1967) and *M. rume* (Kramer 1990: 62), long known to generate unusually strong EODs which can be felt with wet fingers. The field equipment used in the present study was not designed to measure EOD amplitudes, which would have required a strict recording geometry with an immobile, though fully conscious, fish. The EOD of *M. hasselquistii* was so strong that this species was painful for the researcher to handle, being more similar to an electric fence charge than that of a weakly electric mormyrid fish (personal observation).

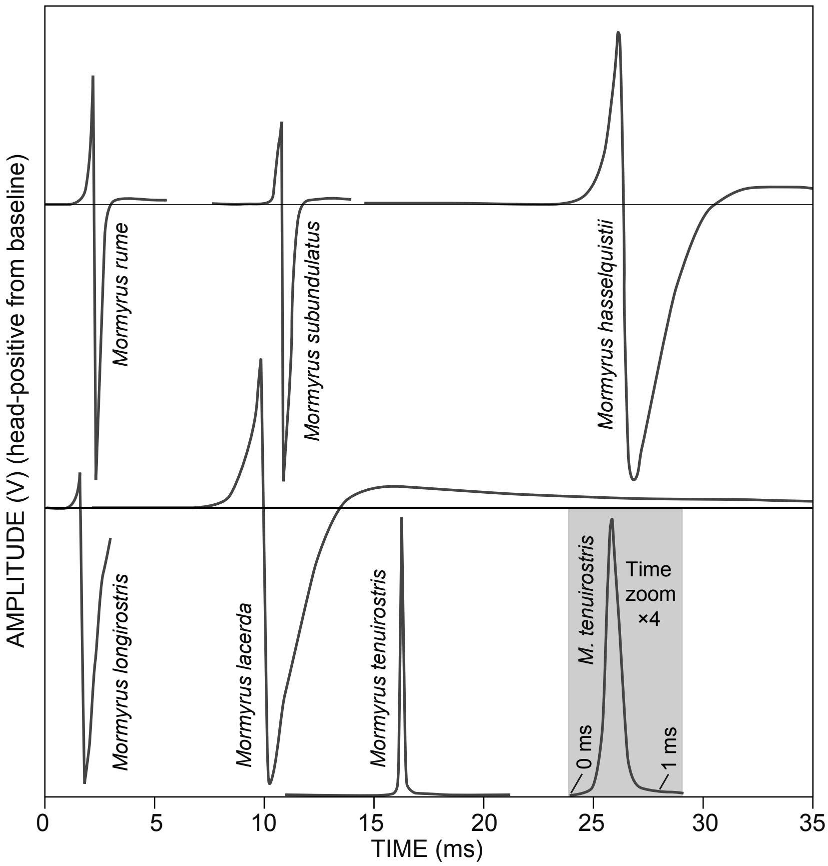

Figure 7: Diagrams of EODs from several African *Mormyrus* species. Head-positivity is upwards. Main potential scaled to 1 volt, which is head-negative in all but *M. tenuirostris* where it is head-positive. Same time-scale for all EODs, except for inset (grey background) which is ×4. Baselines indicate 0 V in both upper and lower panels. Upper panel: West African species; lower panel: southern and East African species. The incomplete recording of an EOD attributed to *M. longirostris* was made *in situ* in the Lower Zambezi River at Tete of a fish that was neither seen nor caught

The recording apparatus detected *M. hasselquistii*'s EOD not only on its own, but also in fishless water-filled buckets some distance away, and similarly when a single mormyrid, such as *Marcusenius* sp., seemed to generate two different EOD waveforms at independent rates when an *M. hasselquistii* was kept in a separate bucket nearby. *Mormyrus hasselquistii* is physically a much stronger fish when compared to an *M. rume* of similar size (Figure 8).

Another surprising finding, and something hitherto unknown to science, was the discovery of a purely monopolar EOD in *M. tenuirostris*. This EOD was head-positive without even a trace of a head-negative pre- or after-potential, such as observed in the essentially monopolar EODs of the Upper Zambezi species complex of *Hippopotamyrus ansorgii* and *H. szaboi* (Kramer et al. 2004). Thus the *M. tenuirostris* EOD waveform is totally different from all other known *Mormyrus* EODs, besides being unusually short: 362 ± 14 μs (N = 4) at 10% pulse amplitude (Figure 7).

The hypothesis of there being a sex difference in the EOD characteristics of *M. subundulatus* is suggested by its rather high coefficient of variation (CV, i.e. ratio of the standard deviation to the mean, given as percent) of EODdur of 19.9%. However, a MANOVA test including all seven waveform characters (in Appendix 3, excepting EODdur to avoid redundancy with its constituents, P1dur and Ndur) yielded an insignificant result, i.e. no support for a sex difference ($F_{7,3}$ = 0.759; p = 0.6577 for all four test variables, Wilks' lambda, Roy's greatest root, Hotelling-Lawley trace and Pillai trace). This was confirmed by subsequent univariate ANOVAs that also found no differences among any of the characters tested ($F_{1,9} \leq 2.018$; $p \geq 0.1892$). In contrast, the EOD characteristics of syntopical *M. rume* (N = 11) sampled at the same time and place, with a CV of 28.7% in EODdur, differed significantly between the sexes (MANOVA on all EOD waveform variables in Appendix 3 except EODdur; $F_{7,2}$ = 22.395; p = 0.0434; same for all four test variables). This result was due to the significantly higher Ndur and Narea values observed in males than in females (Ndur: $F_{1,8}$ = 6.467, p = 0.0345; Narea: $F_{1,8}$ = 8.617, p = 0.0189; univariate ANOVAs). The Ndur mean was 848.4 ± 128 μs in females and 1 489 ± 246.2 μs in males, and thus was almost twice as long in males. Narea was 322.8 ± 40 V × μs in females and 486.6 ± 31.6 V × μs in males. The EOD duration (EODdur) averaged 1 334 ± 106 μs in females vs 2 008 ± 195 μs in males. All seven characters of the *M. rume* sample from the Comoé River (N = 6, at least five being females; Appendix 3) closely resembled those of the female values from the

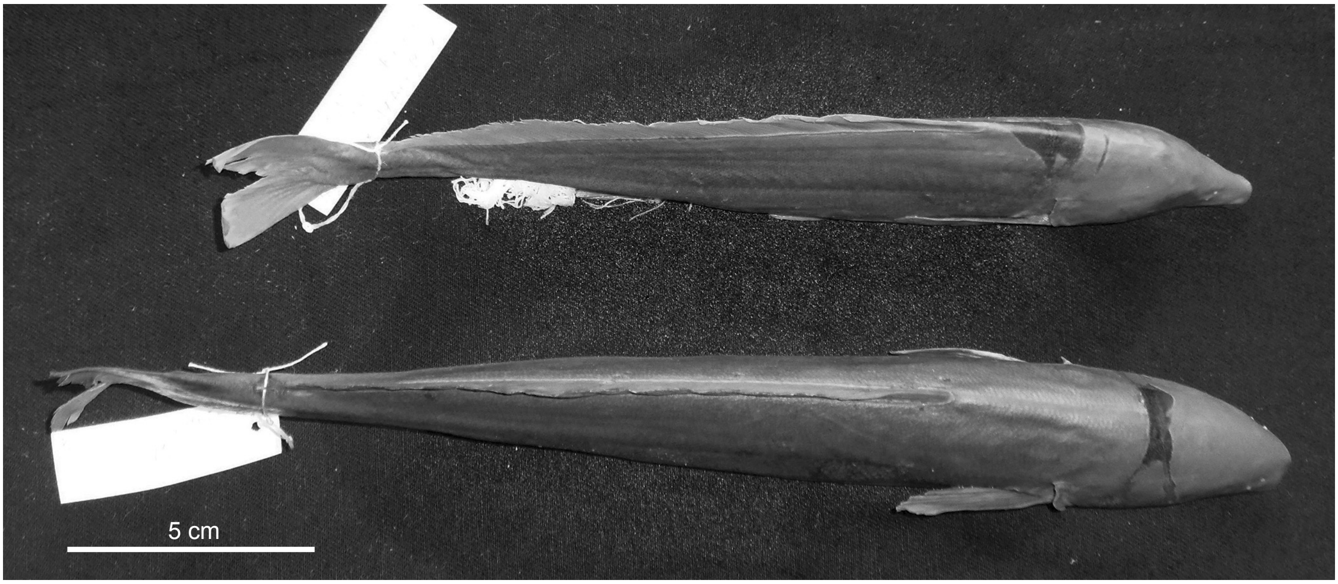

Figure 8: *Mormyrus rume* (top) and *M. hasselquistii* (25 cm SL, below) viewed from above

Bandama sample, i.e. no significant differences. In the PCA the sex difference was visible in *M. rume*, but not in *M. subundulatus* (Figure 9). Notwithstanding their great morphological similarity, in terms of PC and especially of DA, the two species' EODs proved distinct when compared to that of *M. lacerda* (i.e. non-overlapping confidence circles, Figure 10).

Specimens of a second sample of *M. rume* (N = 6) from the independent Comoé River, all being females except one, the sex of which could not be determined, showed yet higher average P1amp scores, but somewhat lower EODdur scores than the Bandama specimens (Appendix 3). The Comoé sample overlapped the Bandama sample in both PCA and DA, and hence there is no reason to assume differentiation (Figure 10). The two Côte d'Ivoire species, *M. rume* and *M. subundulatus*, were strongly differentiated from the various southern African samples of *M. lacerda* on PC1, except for *M. hasselquistii*, the scores of which were close to, but distinct from, the southern African species. Scores for the various *M. lacerda* samples were widely scattered along PC2, and therefore the question of EOD differentiation among them cannot be conclusively resolved at present for lack of more numerous samples from the Kwando, Okavango and Cunene rivers.

The next highest coefficient of variation for EODdur was 12.1% in *M. lacerda* from the Upper Zambezi, and was considerably lower for the remaining species and samples. No further significant sex differences emerged from any of the present data.

The Lower and Middle Zambezi River is inhabited by *M. longirostris* Peters 1852, whereas *M. lacerda* is restricted to the Upper Zambezi (Skelton 2001). It was not possible to catch specimens of *M. longirostris*, but its EODs were recorded *in situ* from fish hiding in dense reed beds 3 m offshore in the Lower Zambezi at Tete during the day. This was done by cautiously moving an electrode set mounted on a long wooden pole to near the spot from which strong signals had been located by an electronic audio device. Because bright sunlight blanched the oscilloscope screen, the result was a 'blind' recording: an unnecessarily high sweep speed (i.e. a short recording time window), which is suitable for other mormyrid species, was inadvertently used, and therefore the latter part of the EODs of *M. longirostris* was clipped (Figure 7). Attempts at making nocturnal recordings were unsuccessful because the fish had dispersed and their constant moving about made recording difficult. In spite of the shortcomings of these recordings, of specimens that had neither been seen nor properly identified, they clearly betrayed the presence of what must have been *M. longirostris*. The EODs showed a *Mormyrus* discharge waveform similar to that of *M. lacerda* which, although shorter than that of the latter species, lasted much longer than the EODs of all other mormyrid species in this part of the river the EODs of which are known, such as *M. macrolepidotus*: Kramer et al. 2007; *Cyphomyrus discorhynchus*: Kramer and van der Bank 2011; and *Mormyrops anguilloides*: BK unpublished data. The putative *M. longirostris* EOD also differed from that of *M. lacerda* by a very low P1 phase amplitude (12.7% of N phase amplitude in the former vs a mean of 58.2% in the latter) of short duration (1.36 ms at '5% criterion' in the former vs a mean 2.45 ms in the latter). At corresponding points of the clipped N phase, the duration of the N phase of *M. longirostris* was 1.36 ms vs 2.72 ms in *M. lacerda* (Figure 7).

Amplitude spectra confirmed that the EODs of *Mormyrus* species occupy the very low-frequency range among mormyrids (Figure 11). The EODs of *M. subundulatus* showed weak peaks slightly rising above the lower frequencies. These peaks were at 119.5 and 543 Hz for the longest and the shortest EODs in the sample, respectively. On the high-frequency side, −10 dB values occurred at 1 456 and 2 452 Hz, respectively. The longest EOD of *M. rume* showed no attenuation throughout a wide low-frequency range, with −10 dB attenuation occurring only at 1 537 Hz. The shortest EOD peaked at 538 Hz, and the −10 dB frequency value

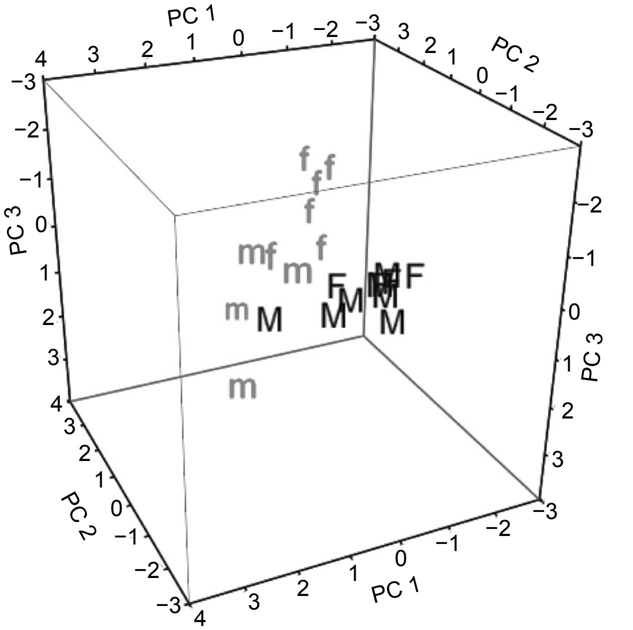

Figure 9: Principal components analysis for the EODs of two *Mormyrus* species from the Bandama River. *Mormyrus rume*: m = males, f = females; *M. subundulatus*: M = males, F = females. Analysis based on seven EOD characters: P1amp, P2amp, P1dur, Ndur, P1Nsep, P1area, Narea. Note segregation of points for the two sexes in *M. rume*

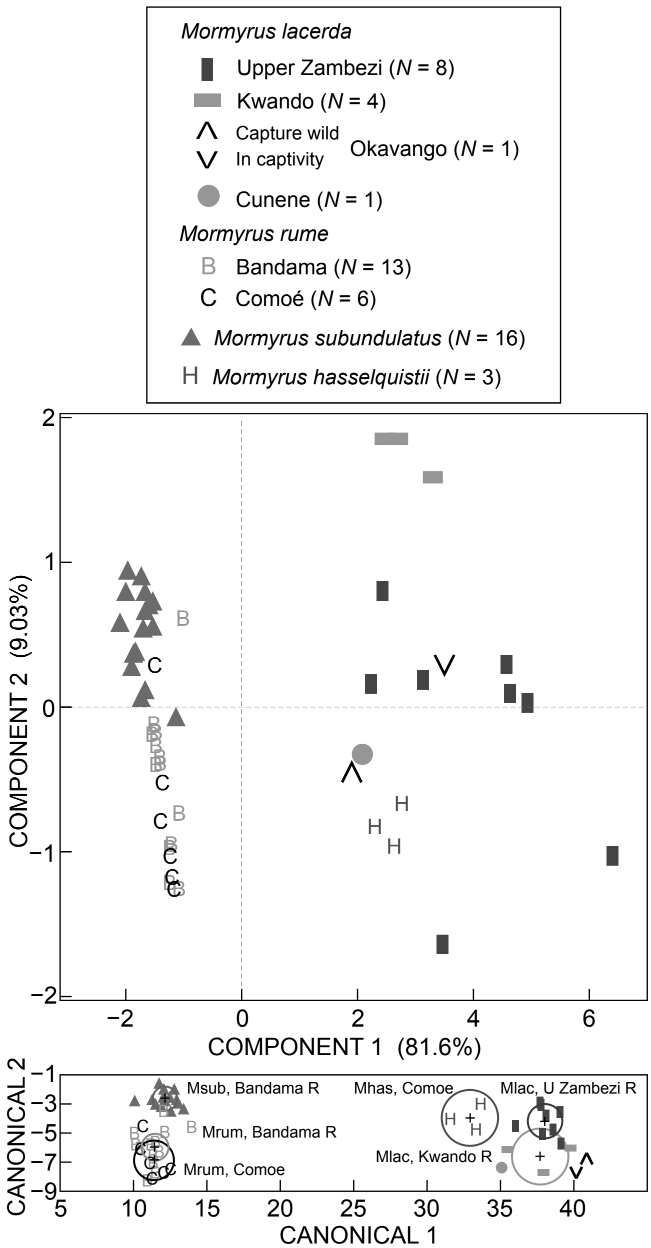

Figure 10: Principal components analysis and discriminant analysis (DA) on the EODs of *Mormyrus* species (seven characters shown in Appendix 3, with EODdur excluded): *M. rume* (Bandama River and Comoé River); *M. subundulatus* (Bandama River); *M. hasselquistii* (Comoé River); *M. lacerda* (Upper Zambezi River, Kwando River and Cunene River). Excluded from DA analysis but position on graph shown: *M. lacerda* (Okavango River: when caught wild in 2004, and in captivity 2009, respectively; same specimen)

was observed at 3 356 Hz. The present study's specimens thus showed EODs the spectral amplitude peaks of which were far below 1 kHz. This is in contrast to the spectra shown by Crawford and Hopkins (1989) which did not show the range below 100 Hz.

The EOD amplitude spectra of *M. lacerda* had pronounced peaks (PPFs) at 34.7 and 91.8 Hz for the longest and the shortest EODs, respectively. Similarly, low PPF values (below 70 Hz) were also observed in *M. hasselquistii* that were markedly stronger in the very lowest frequency range, in agreement with their pronounced shocking power. Both species' −10 dB frequencies were considerably lower than those of *M. subundulatus* and *M. rume*: 357 and 568 Hz for the longest and the shortest EODs in *M. lacerda*, respectively, and 530 and 649 Hz, respectively, in *M. hasselquistii*. The flat spectra of the relatively short, purely monopolar EOD pulses of *M. tenuirostris* only levelled off at 2 651 and 3 188 Hz (−10 dB values for the longest and shortest EODs in the sample; Figure 11d). These very brief DC pulses were too weak to hurt one's wet fingers.

Differences between the two studies of M. rume *and* M. subundulatus *EODs*

Temperature was probably not a significant factor in explaining the differences between the two studies in EOD pulse duration. At 25.23 °C (SD 1.2), the average temperature in Crawford and Hopkins' (1989) study was similar to that in the present study, where EOD duration was normalised to 25 °C if necessary. There remain the possibilities of ontogeny, or else a recording artefact associated with the use of a magnetic tape recorder, as employed by Crawford and Hopkins (1989), as confounding factors. Tape-recording EOD pulses may dramatically alter their waveform, depending on pulse duration, spectral frequency content, tape recorder type, recording speed, and magnetic tape specifications, even when using the best equipment available (Kramer and Weymann 1987). This is because the

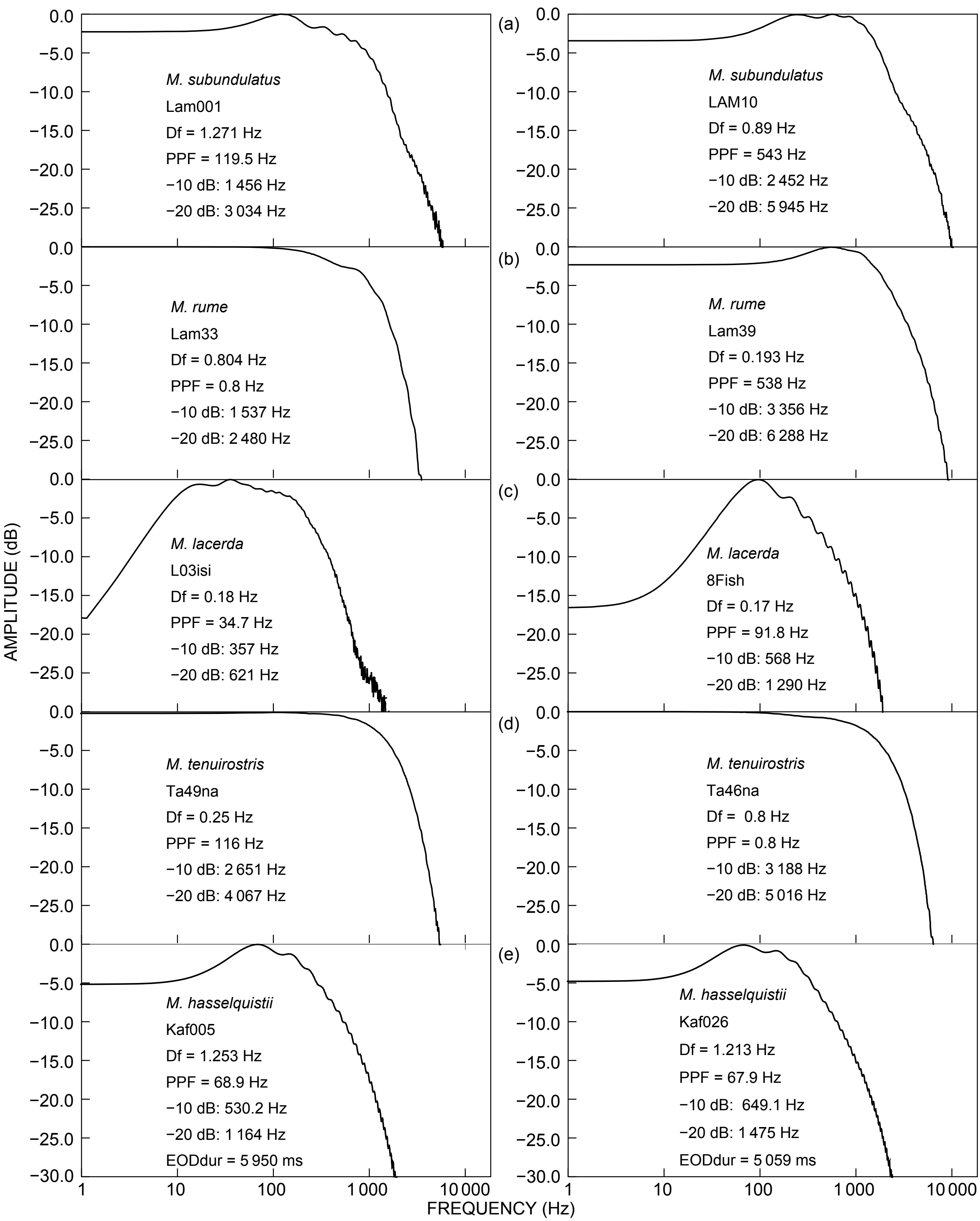

Figure 11: Amplitude spectra of single EOD pulses of *Mormyrus* species. Amplitudes relative to the strongest spectral signal component = 0 dB. Note logarithmic abscissa for frequency in Hz. Left, a species' longest EOD; right shortest EOD. (a) = *M. subundulatus*; (b) = *M. rume* (Bandama sample); (c) = *M. lacerda* (Upper Zambezi sample); (d) = *M. tenuirostris*; (e) = *M. hasselquistii*. Df, frequency resolution; PPF, peak power frequency; frequencies at −10 dB and −20 dB re: 0 dB on the high-frequency side

'direct' tape recording procedure differentially phase-shifts spectral components of the recorded signal.

Even though the EOD waveform recordings appeared good enough to the researchers, this explanation cannot be ruled out without further study. However, such an effect, if present, does not invalidate Crawford and Hopkins' (1989) conclusion that there were two groups of *Mormyrus* fish that differed in EOD waveform: *M. rume* and an unknown species (their new species *M. subundulatus*), as the same recording procedure had been applied to both species.

The possibility of ontogenetic development as one reason for the differences between the two studies is supported by the great size differences between the two studies' specimens, especially for *M. subundulatus*. The *M. subundulatus* specimens in the present study were on average much more than twice the size of those used in the 1989 study (22.5 cm, SD 1.2, *N* = 11 vs 8.48 cm, SD 4, *N* = 5), whereas the *M. rume* specimens in the present study were on average slightly less than twice the size of those in the 1989 study (29.7 cm, SE 1.6, *N* = 11 for the Bandama specimens alone, compared to 15.5 cm, SD 4.2, *N* = 9 for the 1989 study). Ontogenetic change was clearly observed in one 11.7 cm SL *M. lacerda* specimen (field no. 147) in the present study, caught in the Okavango Delta. After it had grown to 30 cm SL in captivity, the relative P1 amplitude of its EOD had increased by 16% from 0.431 to 0.499 and the total EOD pulse duration by 5%. Therefore, growth probably explains some of the differences between the EODs of *M. subundulatus* and *M. rume* recorded in the two studies.

Discussion

The present study shows the EODs of five *Mormyrus* species that were all digitised and numerically stored immediately after capture in the field. It demonstrates a sex difference in the EOD of *M. rume* and demonstrates the great homogeneity of *Mormyrus* species across Africa, both in morphological and electrical phenotype. With one exception, all species studied generated long, biphasic EODs of similar waveform, although variable in duration and strength. *Mormyrus tenuirostris* from Kenya is a notable exception, having a purely monophasic, very short DC pulse. Morphologically, *M. tenuirostris* is exceptional for its longer head, shorter dorsal fin with fewer rays than its congeners and a dorsal fin origin positioned behind that of the pelvic fins. It would be interesting to explore what caused *M. tenuirostris* to differentiate so strongly from its congeners in evolution.

Another notable finding was the great strength of the EOD pulses of *M. hasselquistii*. For a mormyrid with a sophisticated electrocommunication and electrolocation system, which must also be assumed for *M. hasselquistii*, it would appear counterproductive to generate EODs so strong they are painful to a human handling the fish, and probably also to other non-electroreceptive organisms if sufficiently close. Neither 'private' communication, clandestine electrolocation, or even 'electrofishing' (i.e. immobilising prey by electroshocking) appear to be possible, because the EODs of *M. hasselquistii* are almost certainly too strong for the first two functions, but probably not strong enough for the last. It is unknown whether or not *M. hasselquistii* can electrically disable prey organisms, as can the electric catfish *Malapterurus*. They might, however, deter predators, even though the fish appears to be so sturdy and strong that, from a certain size upwards, it might not need such protection. Their unexpected EOD strength requires additional research.

Even though the 'blind' *in situ* EOD recording of the EOD of a putative *M. longirostris* in the Lower Zambezi was clipped at its phasing out (Figure 7), it clearly shows that differentiation from the Upper Zambezian species, *M. lacerda*, is not limited to morphology but includes the EOD.

Principal component analysis revealed pertinent features of value in *Mormyrus* taxonomy. It is tempting to speculate that the variation in strength of the EODs of *Mormyrus* is correlated with caudal peduncle depth, the character that loaded PC1 most strongly. A fisherman reported that *M. subundulatus* shocks more strongly than *M. rume* (Roberts 1989), the caudal peduncle of the former being deeper, whilst *M. hasselquistii* also has a deep caudal peduncle. A more quantitative measure of EOD voltage and current output, or shocking strength, is desirable for future studies.

The present study has confirmed the validity of *M. subundulatus*, a syntopical sibling species to *Mormyrus rume* discovered in the Bandama River, Côte d'Ivoire (Crawford and Hopkins 1989, Roberts 1989). The present study has added information on electrical and morphological characteristics of the two sibling species. The EODs of *M. rume* and *M. subundulatus* of a more mature size were substantially longer in the present study than in that of Crawford and Hopkins (1989), and the P1 phase amplitudes of the EODs of *M. subundulatus* were twice as strong. However, there was no notable difference in the P1 phase amplitudes for *M. rume*. These and other quantitative differences could be due to ontogenetic development, temperature difference, or recording artefact. Ontogenetic growth definitely partly explains the differences between the EODs of *M. subundulatus* and *M. rume* recorded in the two studies.

A longer average EOD duration in *M. rume* than in *M. subundulatus* is explained by a sex difference in the former: the N phase duration in male *M. rume* was almost twice that of females. No such sex difference was observed in any of the other *Mormyrus* species.

In order to describe the marked degree of differentiation and its evolution within the genus *Mormyrus* across Africa, many more rivers and lakes need to be sampled for this genus. Especially needed are samples from Central Africa and Angola, and from East Africa and north-eastern Africa.

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Appendices: Morphological and electrical differences between samples collected

Appendix 1: Morphological measures for samples of different *Mormyrus* species or populations from various origins. SE = standard error; median and SIQ (semi-interquartiles), for count measures (nD, nA, SPc, SLS). Refer to Figure 2 for localities. Bold type indicates data from Bigorne's (2003) reference work

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 peduncle
CPL = length of caudal peduncle (from end of anal fin base to midbase of caudal fin)
CPD = depth of caudal peduncle (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 centres of the pair of nares on one side
OD = eye diameter as defined by the orbital rims
LPF = length of the left pectoral fin
PPF = distance from the origin of the pelvic fin to the origin of the anal fin (for the more recent specimens)
SL = standard length (distance from the tip of the snout to the midbase of the caudal fin)
BD = body depth (the greatest vertical distance across the body)
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 by Skelton (2001: 67) (range of accuracy ±2 counts)

	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)
M. lacerda, Upper Zambezi River																				
Mean/median	0.4051	0.6656	0.5172	0.1346	0.6112	0.2325	0.6550	0.2422	0.3197	0.4582	0.4074	0.1320	0.2470	20.28	0.2299	64.5	20	20	87.5	25.9
Min.	0.3801	0.6476	0.4964	0.1270	0.5952	0.2210	0.6430	0.2325	0.3099	0.4394	0.3864	0.1220	0.2313	18.80	0.2134	62	19	20	86	21.3
Max.	0.4293	0.6905	0.5371	0.1425	0.6643	0.2426	0.6661	0.2532	0.3281	0.4818	0.4227	0.1445	0.2670	23.56	0.2753	67	21	20	89	35.5
SE/SIQ	0.0066	0.0052	0.0046	0.0022	0.0079	0.0029	0.0030	0.0028	0.0024	0.0047	0.0041	0.0031	0.0047	0.5611	0.0079	1.25	0.75	0	1	1.65
N	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8
M. lacerda, Kwando River																				
Mean/median	0.3913	0.6697	0.4864	0.1262	0.5664	0.2379	0.6305	0.2196	0.3452	0.4639	0.4029	0.1374	0.2394	19.28	0.2353	62	20	20	88.5	30.7
Min.	0.3788	0.6495	0.4617	0.1209	0.4967	0.2165	0.6165	0.2084	0.2948	0.4446	0.3920	0.1327	0.2328	17.92	0.2209	61	19	20	86	28.5
Max.	0.4052	0.6932	0.4998	0.1333	0.6124	0.2511	0.6457	0.2377	0.3672	0.4899	0.4199	0.1410	0.2491	19.86	0.2457	66	20	22	89	34.0
SE/SIQ	0.0070	0.0091	0.0086	0.0026	0.0259	0.0075	0.0064	0.0065	0.0171	0.0099	0.0061	0.0017	0.0035	0.4586	0.0052	1.25	0.25	0.5	1	1.18
N	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4
M. lacerda, Cunene R	0.3788	0.6708	0.4998	0.1333	0.6124	0.2402	0.6457	0.2377	0.2948	0.4899	0.4199	0.1410	0.2328	17.92	0.2457	66	19	22	89	28.5
N	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
M. tenuirostris, Tana River																				
Mean/median	0.4787	0.6197	0.4524	0.1252	0.5225	0.1880	0.5849	0.2706	0.2387	0.5289	0.4924	0.1293	0.2981	20.52	0.2397	57.5	20	25	90.5	21.5
Min.	0.4590	0.5915	0.4362	0.1237	0.4880	0.1794	0.5644	0.2382	0.1800	0.5147	0.4797	0.1268	0.2905	19.68	0.2106	56	19	24	87	19.3
Max.	0.4985	0.6420	0.4659	0.1271	0.5440	0.1992	0.6001	0.3202	0.2831	0.5439	0.5093	0.1338	0.3073	21.69	0.2575	64	21	26	95	24.8
SE/SIQ	0.0081	0.011	0.0061	0.0007	0.0131	0.0046	0.0075	0.0177	0.0214	0.0064	0.0066	0.0016	0.0041	0.4234	0.0104	2.25	0.5	1	2.25	1.30
N	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4
***M. rume* (West Africa) Bigorne 2003**																				
Min.			**0.476**	**0.090**								**0.147**	**0.185**		**0.164**	**72**	**16**	**20**	**92**	
Max.			**0.588**	**0.114**								**0.204**	**0.270**		**0.286**	**95**	**21**	**26**	**115**	
M. rume, Bandama River																				
Mean/median	0.3680	0.5875	0.5498	0.0937	0.6305	0.1805	0.6703	0.3159	0.1563	0.5949	0.5323	0.1472	0.2265	23.83	0.1926	83	19	22	105	28.0
Min.	0.3340	0.5389	0.5131	0.0832	0.5679	0.1575	0.6434	0.2952	0.1346	0.5786	0.5125	0.1244	0.2007	19.30	0.1629	72	16	18	93	21.4
Max.	0.3891	0.6109	0.5870	0.1047	0.6959	0.1978	0.7063	0.3387	0.1906	0.6181	0.5954	0.1803	0.2415	27.11	0.2191	87	20	22	109	40.0
SE/SIQ	0.0038	0.0057	0.0055	0.0016	0.0094	0.0028	0.0049	0.0039	0.0034	0.0031	0.0051	0.0039	0.0029	0.5665	0.0045	2.25	0.5	0.875	1.875	1.38
N	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15

Appendix 1: (cont.)

	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)
M. rume, Comoé River																				
Mean/median	0.3657	0.5899	0.5826	0.0959	0.7009	0.1900	0.6979	0.3259	0.1463	0.6091	0.5311	0.1641	0.2226	22.74	0.2106	84	18.5	20	101.5	23.3
Min.	0.3614	0.5737	0.5667	0.0905	0.664	0.1854	0.6724	0.3128	0.1314	0.6007	0.5156	0.1415	0.2170	19.81	0.1948	83	18	20	92	18.4
Max.	0.3697	0.6090	0.6142	0.0997	0.7388	0.1945	0.7327	0.3435	0.1548	0.6141	0.5381	0.1782	0.2316	27.03	0.2204	89	19	22	106	31.0
SE/SIQ	0.0014	0.0047	0.007	0.0015	0.0098	0.0017	0.0081	0.0049	0.0032	0.0023	0.0034	0.0058	0.0023	1.2232	0.0038	2	0.5	0	3.5	2.27
N	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6
***M. hasselquistii* (West Africa) Bigorne 2003**																				
Min.			**0.526**	**0.087**								**0.120**	**0.185**		**0.161**	**63**	**16**	**26**	**84**	
Max.			**0.588**	**0.135**								**0.149**	**0.233**		**0.238**	**82**	**20**	**34**	**100**	
M. hasselquistii, Comoé River																				
Mean/median	0.3476	0.6302	0.5618	0.1263	0.6691	0.2335	0.6821	0.2562	0.2530	0.4819	0.3998	0.1597	0.2089	15.72	0.1897	68	18	30	96	24.1
Min.	0.3396	0.6245	0.5507	0.1193	0.6591	0.2313	0.6748	0.2493	0.2374	0.4710	0.3900	0.1443	0.2029	15.26	0.1830	67	18	28	94	22.9
Max.	0.3535	0.6356	0.5719	0.1311	0.6776	0.2373	0.6910	0.2644	0.2644	0.4885	0.4084	0.1766	0.2120	16.14	0.1944	69	19	30	97	24.9
SE/SIQ	0.0041	0.0032	0.0061	0.0036	0.0054	0.0019	0.0047	0.0044	0.0081	0.0055	0.0053	0.0093	0.0030	0.2541	0.0034	0.75	0.375	0.75	1.125	0.61
N	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3
***M. subundulatus* (West Africa) Bigorne 2003**																				
Min.																**60**	**16**	**21**	**87**	
Max.																**71**	**18**	**26**	**99**	
M. subundulatus, Bandama River																				
Mean/median	0.4006	0.6018	0.5188	0.103	0.5745	0.1757	0.6513	0.3032	0.1896	0.6068	0.5257	0.1633	0.2478	24.03	0.2010	65	17	20	88.5	22.5
Min.	0.3733	0.5553	0.4943	0.0902	0.4818	0.1589	0.6279	0.2909	0.1668	0.5773	0.5165	0.1215	0.2186	20.89	0.1688	60	16	20	87	15.0
Max.	0.4274	0.6284	0.5501	0.1148	0.6242	0.1908	0.6844	0.3145	0.2112	0.6265	0.5372	0.1833	0.2662	27.07	0.2273	70	18	22	92	33.3
SE/SIQ	0.0033	0.0038	0.0039	0.0016	0.0122	0.0022	0.0040	0.0022	0.0027	0.0034	0.0017	0.0044	0.0027	0.5168	0.0037	1.75	0.375	0	1	1.20
N	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16	15	16	16	16

Appendix 2: Principal components analysis on correlations for 19 morphological characters of specimens of *Mormyrus* species from Africa. For abbreviations, see Appendix 1

Eigenvalue	9.4099	3.7665	1.3856	1.2614	1.0616	0.5654	0.411
Percent	49.526	19.824	7.292	6.639	5.587	2.976	2.163
Cumulative percent	49.526	69.349	76.642	83.281	88.868	91.843	94.007
				Component loadings			
PDL/SL	−0.59839	−0.66544	0.20033	0.10763	0.28006	0.15654	−0.07035
PAL/SL	−0.85806	0.24826	0.21183	−0.20422	0.01733	0.13185	0.16119
LD/SL	0.68459	0.58985	0.19318	−0.15533	0.20448	0.22521	0.02160
LA/SL	−0.90754	0.18819	−0.00091	−0.05595	0.07724	0.19565	−0.11349
LPF/HL	0.45826	0.71276	0.06195	−0.03222	0.20519	−0.02428	−0.34328
PPF/SL	−0.73824	0.59043	0.05019	−0.09921	0.03900	0.08355	0.18995
pD/SL	0.60597	0.62453	0.19041	−0.27185	0.07122	0.27673	−0.07221
CPL/SL	0.90045	−0.21554	0.12050	0.05773	0.17214	0.15400	−0.07113
CPD/CPL	−0.93944	0.21595	0.00439	−0.12750	−0.17035	−0.07157	−0.00116
LSc/HL	0.83327	−0.47455	0.13875	0.05659	0.13166	−0.04597	−0.01900
LSo/HL	0.86852	−0.43030	−0.00703	−0.08396	0.11841	−0.05706	0.03995
OD/HL	0.47409	−0.07693	−0.26183	−0.55370	0.50962	−0.23264	0.19432
HL/SL	−0.54004	−0.69038	0.21426	0.09841	0.30889	0.15812	−0.14375
HL/Na	0.53348	−0.47247	0.36449	−0.09404	−0.37721	0.26274	0.20507
BD/SL	−0.69146	−0.06954	0.44967	−0.03227	0.40738	−0.06059	0.17838
nDges	0.79701	0.41594	0.26536	0.23721	0.02995	−0.08567	0.11331
nAges	−0.54599	0.34332	0.42158	0.41744	0.16414	−0.27984	−0.03005
SPc	−0.17267	0.15838	−0.68403	0.49144	0.32421	0.28041	0.15191
SLS	0.71894	0.31935	0.14586	0.51774	0.00897	−0.00725	0.17736

M. hasselquistii, Comoé River, *N* = 3; *M. lacerda*, Kwando River, *N* = 4; *M. lacerda*, Upper Zambezi River, *N* = 8; *M. rume*, Bandama River, *N* = 15; *M. rume*, Comoé River, *N* = 6; *M. subundulatus*, Bandama River, *N* = 15; *M. tenuirostris*, Tana River, *N* = 4

Appendix 3: Characters of the EOD pulse waveform of *Mormyrus* species and populations from various origins. Amplitudes re: Namp = |1| V

Namp = head-negative peak amplitude of N phase (measured from baseline to minimum, which was equal to −1 V by definition)
P1amp = peak amplitude of positive P1 phase (re: Namp)
P2amp = positive peak amplitude of post potential
Ndur, P1dur = durations of respective phases
P1Nsep = separation or interval between peaks of P1 and N phases
P1area, Narea = areas under the P1 and N phases, respectively
EODdur = total EOD duration
SL = standard length

	P1amp (V)	P2amp (V)	P1dur (µs)	Ndur (µs)	P1Nsep (µs)	P1area (V × µs)	Narea (V × µs)	EODdur (µs)	EODdur (CV%)	SL (cm)
M. lacerda, Upper Zambezi River										
Mean	0.582	0.081	2 447.9	4 227.4	864.1	492.3	1 935.8	6 675.3	12.1	27
Min.	0.424	0.020	2 042.8	3 337.6	400	361.9	1 459.6	5 380.4		23
Max.	0.779	0.101	2 931.2	5 501.1	1 400	667	2 530.2	7 968.1		38.5
SE	0.035	0.009	122.3	251.1	130.4	41.54	127.4	285		1.8
N	8	8	8	8	8	8	8	8		8
M. lacerda, Kwando River										
Mean	0.534	0.148	2 308.2	2 868.2	515.3	369.2	1 279.4	5 176.4	4.8	31.5
Min.	0.499	0.141	2 109.7	2 538.5	482	337.4	1 121.1	4 974.2		29.7
Max.	0.593	0.155	2 490.1	3 201.6	564	418.1	1 443.8	5 526.5		34
SE	0.03	0.004	110.1	191.4	24.9	24.8	93.2	175.7		1.3
N	3	3	3	3	3	3	3	3		3
M. lacerda 147, Okavango										
(wild, 2004)	0.431	0.024	2 598.3	4 061.2	379	338.4	1 526.6	6 659.5	–	11.7
(in captivity, 2009)	0.499	0.0664	3 483.4	3 511	560	600.7	1 582.2	6 994.4	–	30
N	1	1	1	1	1	1	1	1		1
M. lacerda, Cunene River	0.606	0.067	2 130.2	3 104.6	359.9	350.1	1 288.9	5 234.8	–	30.3
N	1	1	1	1	1	1	1	1		1
M. tenuirostris, Tana River										
Mean	1.00	–	362.3	–	–	–	–	362.3	7.8	22.4
Min.	1.00	–	330	–	–	–	–	330		19.8
Max.	1.00	–	398.9	–	–	–	–	398.9		25.9
SE	0	–	14.13	–	–	–	–	14.13		1.49
N	4	–	4	–	–	–	–	4		4
M. rume, Bandama River (all)										
Mean	0.425	0.018	486.6	1 068.6	181.3	78.8	379.9	1 555.2	27.4	28.58
Min.	0.318	0	381	657	103.9	63.4	253.5	1 156.4		21.4
Max.	0.574	0.053	715.7	1 977.2	320	98.7	557.3	2 454.6		40
SE	0.018	0.004	23.52	125.8	16.8	2.39	32.2	118.1		1.52
N	13	13	13	13	13	13	13	13		13
M. rume, Bandama River (♂♂)										
Mean	0.398	0.014	518.7	1 489	234.3	85.5	468.6	2 007.8	19.4	32
Min.	0.358	0.0	402.6	898.3	180	72.8	406.5	1 614		27.5
Max.	0.443	0.053	715.7	1 977.2	320	98.7	557.3	2 454.6		36.8
SE	0.021	0.013	68	246.2	31.5	37.1	31.6	194.6		2.1
N	4	4	4	4	4	4	4	4		4
M. rume, Bandama River (♀♀)										
Mean	0.432	0.02	485.9	848.4	164.3	77.9	322.8	1 334.3	19.5	28.6
Min.	0.369	0	381	657	129.6	75.4	256	1 156.4		22.9
Max.	0.489	0.026	556.1	1 472.9	234	80.5	515.3	1 853.9		40
SE	0.017	0.004	25.3	127.9	17.2	0.83	39.9	106.5		2.5
N	6	6	6	6	6	6	6	6		6
M. rume, Comoé River										
Mean	0.489	0.019	468.8	862.5	145.2	72.2	306.7	1 331.3	13.5	23.3
Min.	0.301	0.011	432.6	688.4	98.4	61.3	235.2	1 128.6		18.3
Max.	0.580	0.028	539.4	1 130.4	246.3	79	375	1 563		31
SE	0.042	0.003	15.74	74.8	22.1	2.7	22.4	73.5		2.3
N	6	6	6	6	6	6	6	6		6
M. hasselquistii, Comoé River										
Mean	0.615	0.055	1 816.3	3 466.4	511.6	381.3	1 577.1	5 282.7	4.3	24.1
Min.	0.595	0.050	1 696.9	3 357.2	475.7	361.4	1 507.9	5 101		22.9
Max.	0.651	0.058	2 008.3	3 531.4	571.3	404.8	1 639.7	5 539.7		24.9
SE	0.018	0.003	96.93	54.9	30	12.7	38.2	73.5		0.6
N	3	3	3	3	3	3	3	3		3
M. subundulatus, Bandama River										
Mean	0.316	0.038	441.2	791.1	148.3	63.7	390.8	1 232.3	19.9	22.5
Min.	0.242	0.022	392.4	587.2	108	53.5	290.9	994.3		15
Max.	0.419	0.053	484.2	1 591	291.6	83.4	540.8	2 048.9		33.3
SE	0.011	0.003	7.434	58.2	11.89	1.8	16.4	61.34		1.2
N	16	16	16	16	16	16	16	16		16