

Morphological and electrophysiological field observations on electric freshwater fish of the genus *Mormyrops* Müller 1843 (Teleostei: Mormyridae) from West and southern Africa

B Kramer

Zoological Institute of the University of Regensburg, Universitätsstrasse 31, D-93040 Regensburg, Germany
e-mail: bernd.kramer@ur.de

Different specimens of *Mormyrops anguilloides* (Linnaeus 1758) were reported to display electric organ discharge (EOD) pulses of either initially head-positive or initially negative polarity, a hypothetical sex difference that has not been substantiated to date. The morphology and EODs of *M. anguilloides* of both sexes and a sexually mature size from the Comoé and Bandama rivers, Côte d'Ivoire, and the Lower and Middle Zambezi, Mozambique, displayed initially positive EODs. The morphologically similar *M. breviceps* Steindachner 1895 of both sexes and a sexually mature size from the Bandama River displayed initially head-negative EODs of biphasic waveform and long duration (0.93–1.15 ms) in the very-low-frequency spectral range. *Mormyrops anguilloides* from the Comoé and Bandama rivers were differentiated in caudal peduncle depth and in EOD waveform, pulse duration and spectral energy content. The former samples displayed a biphasic, lower-frequency EOD pulse of up to 0.42 ms duration, the latter a tetraphasic, high-frequency EOD of up to 0.33 ms. It is suggested that reports of EODs of both polarities in *M. anguilloides* indicate the presence of an unrecognised species.

Keywords: allopatric speciation, amplitude spectra, communication signal, differentiation, electric organ discharges, polarity reversal, sex difference

Introduction

The Mormyridae is the largest freshwater fish family endemic to Africa, and the genus *Mormyrops* holds some of its largest members (1.5 m standard length). From various parts of West Africa and elsewhere, many *Mormyrops* species were described that, after critical comparison, Bigorne (1987) reduced to five. Two of these species, *M. anguilloides* (Linnaeus 1758) and *M. breviceps* Steindachner 1895 (Figure 1), were studied in the present paper.

The Mormyridae all emit electric organ discharges (EODs) for active electrolocation and communication (Kramer 1990, Moller 1995, Kramer 1996, Bullock et al. 2005). The waveforms of EOD pulses are species-characteristic and have been used successfully as taxonomic characters in several genera, e.g. *Mormyrus* (Crawford and Hopkins 1989), *Pollimyrus* (Kramer et al. 2003) and *Hippopotamyrus* (Kramer and Swartz 2010). Gosse and Szabo (1960) obtained a paradoxical result from eight *M. anguilloides* specimens (then termed *M. deliciosus* Leach 1818) from the 'upper Congo basin' (most likely from near Brazzaville, République du Congo; Mme H Szabo, pers. comm.). These fish differed in the polarity of their polyphasic EODs of otherwise similar waveform: the EODs of four specimens were initially head-positive, whereas those of the other four were initially head-negative. The authors traced the polarity difference to an anatomically mirror-symmetrical innervation pattern on either the cranial or the caudal face of the electrocytes that constitute the electric organ. The EOD polarity did not correspond to a morphologically detectable

species difference, and the authors concluded that the eight fish were of the same species. The authors were unable to determine the sex of their specimens, all of which were young (95–140 mm standard length [SL]). This is below the sexually mature size for West African *M. anguilloides* from Mali (first maturity at 325 mm SL) and Côte d'Ivoire (210 mm SL; Paugy 2002).

During a field study on *Mormyrops* specimens in Sierra Leone, West Africa, Moller and Brown (1990) observed short tetraphasic EOD pulses of, on average, 0.471 ms duration that were initially head-positive and, in other specimens, polarity-reversed EOD pulses of biphasic waveform and much longer duration (1.611 ms). All fish appeared to be members of the same species, identified as *M. curviceps* Roman 1966 (i.e. *M. anguilloides*, following Bigorne 1987), and the two EOD types were not related to developmental stage or sex. The authors proposed either the existence of two independent EOD pulse-form morphs in the same species or two cryptic sibling species. Hopkins et al. (2007, reviewing unpublished data) suggest a triphasic EOD for *M. anguilloides* specimens from Cameroon and Mali (West-Central and West Africa, respectively) that was dimorphic: the EODs of some specimens started head-positive, whereas those of others started head-negative. This difference was not related to sex or developmental stage. In a fascinating report on the hunting behaviour of free-ranging *M. anguilloides* in Lake Malawi, Arnegard and Carlson (2005) report that EOD pulse

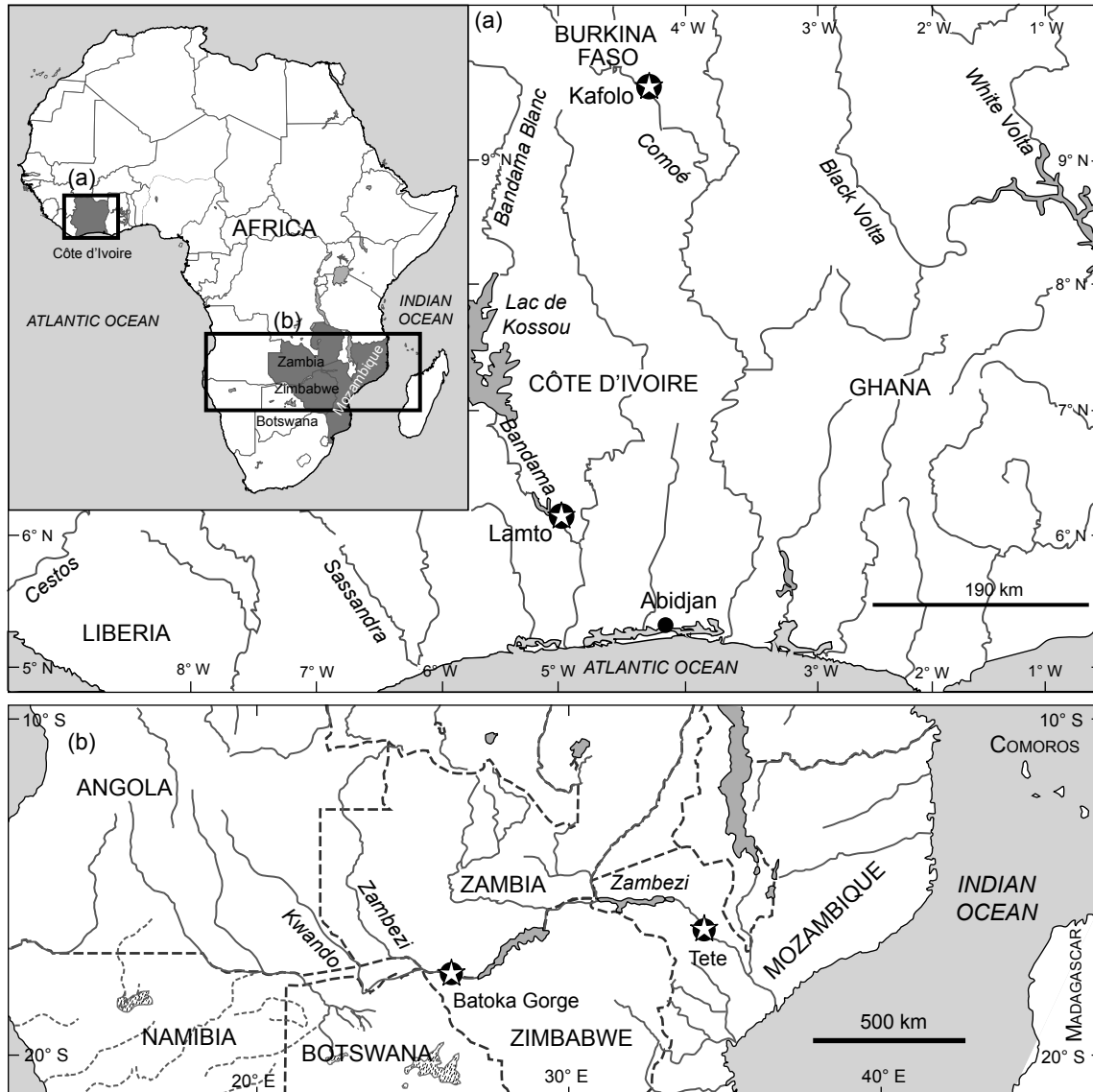


Figure 1: Location of the sample sites. (a) Map of the Bandama and Comoé rivers, Côte d'Ivoire, showing locations of sample sites at Lamto and Kafolo, respectively. (b) Map of the Zambezi River basin, showing locations of sample sites at Tete and the Batoka Gorge

duration ranged from 0.7 to 2.4 ms, without further detail on waveform variation or polarity reversal.

These widely differing and mutually incompatible reports clearly show that the taxonomy and systematics of *Mormyrops anguilloides* needs revision, based on more detailed field studies, both within and between geographic populations. Part of the problem is the very extensive distribution of *M. anguilloides* as presently defined. Following the terminology of ichthyofaunal provinces in Africa, as last reviewed by Lévêque (1997, reprinted in Stiassny et al. 2007: 31), *M. anguilloides* ranges widely across the Nilo-Sudanian, the Upper and Lower Guinean, the Congo and East Coast provinces, and even an eastern part of the Zambezi province, which includes Lake Malawi. The second species studied in the present paper, *M. breviceps*, is restricted to part of West Africa, from the Volta River, Ghana,

in the east to Guinea-Bissau in the west (approximately $0^{\circ}15' E$ to $16^{\circ} W$; estimated from the map in Bigorne 2003).

The present paper offers more quantitative EOD analyses of sexually mature, field-studied specimens, paired with detailed morphological analyses for *M. anguilloides* and *M. breviceps* specimens of a sexually mature size, sampled from two rivers in Côte d'Ivoire. For comparison, field-studied Zambezi specimens of the former species were also included (Figure 2). To the best of my knowledge, this paper offers the first EOD recordings of *M. breviceps*.

Materials and methods

Morphology

Seventeen anatomical measurements (Figure 3) and four counts were recorded for nine specimens from two



Figure 2: Photographs of *Mormyrops* specimens. *Mormyrops anguilloides* from the Comoé River: Kaf014 (SL 39.2 cm), Kaf024 (SL 45.1 cm); *M. anguilloides* from the Bandama River: Lam56 (SL 27.3 cm), Lam62 (SL 19.2 cm); *M. anguilloides* from the Lower Zambezi at Tete: R1 (SL 21.1 cm); *M. breviceps* from the Bandama River: Lam11A (SL 39.8 cm), Lam43A (SL 35 cm). Scale bar = 5 cm

origins in Côte d'Ivoire, and two origins on the Lower and Middle Zambezi in Zambia and Mozambique. The definitions of morphological characters follow mainly those of Kramer (2013a):

PDL = predorsal length (distance from the tip of the snout to the dorsal fin origin)

PAL = distance from tip of snout (= upper lip) 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 the caudal fin)

CPD = depth of caudal peduncle (shortest 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

IOD = inter-orbital distance

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 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)

Measurements were all point-to-point; no projections into other planes were used.

The sex of the Ivorian specimens was recognised by histology, and the stage of egg development determined according to Takashima and Hibiya (1995). In the present *Mormyrops* samples, the 'kink' character of the anal fin base, which indicates the male sex was absent, in contrast to most other mormyrid species, and thus gonad histology was the only reliable way to determine their sex. The gonads were dissected, embedded in paraffin wax, and 7 μm sections were stained following the Azan protocol (Mulisch and Welsch 2010; for details, see Kramer 1997a).

Abbreviations used to represent institutions and collections cited follow Leviton et al. (1985) and Fricke and Eschmeyer (2013). Specimens examined were identified using the dichotomous keys of Lévêque and Paugy (1984), Lévêque et al. (1990) and Bigorne (2003), which are considered effective for fish populations occurring in West Africa. Zambesi specimens were identified following Skelton (2001).

Electric organ discharges

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

Temperature (± 0.1 °C) and water conductivity (± 1 $\mu\text{S cm}^{-1}$) were constantly monitored using an electronic apparatus

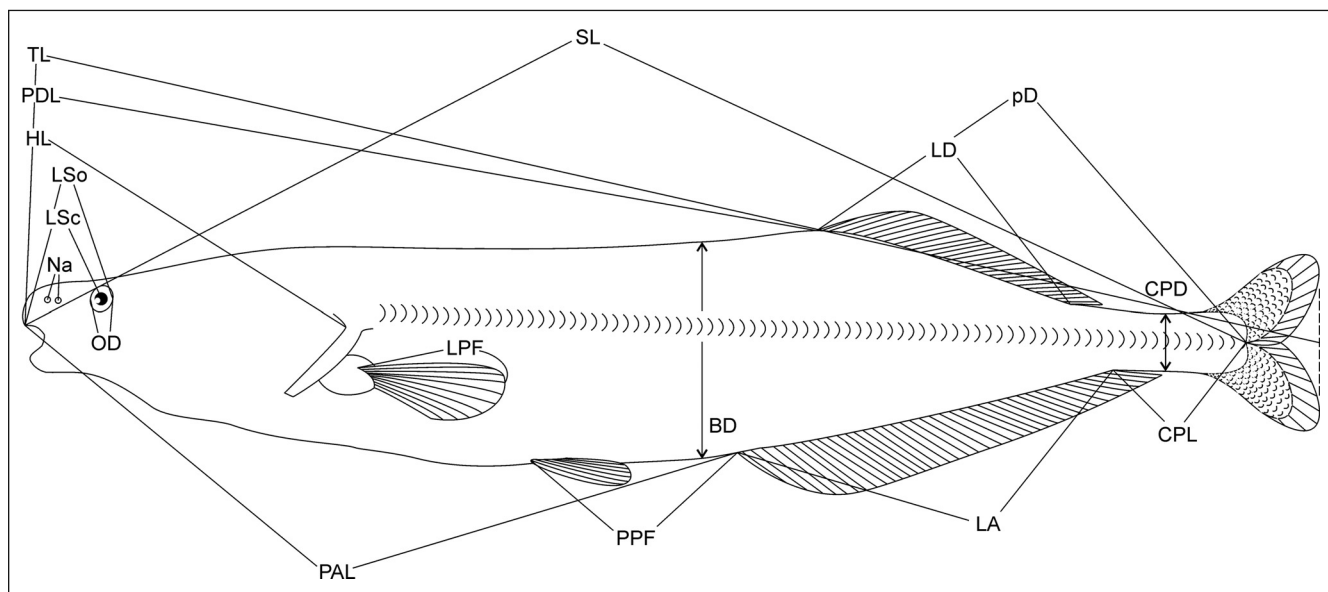


Figure 3: Morphological measurements used in the present study, indicated on a sketch of *Mormyrops anguilloides*. For abbreviations, see the Materials and methods

(LF318 Wissenschaftlich-Technische Werkstätten, Weilheim). 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 to 100 kHz; filter slopes, -3 dB per octave; made in the electronics workshop, Biology Department, University of Regensburg, Regensburg). Amplifier output was recorded with a digital storage oscilloscope (specified to at least 20 MHz/8 bit and either 512, 2 048 or 10 000 points per sweep, depending on the model). Data were numerically transferred onto disk via a digital interface. Usually, four traces per fish were recorded. Except in the first year of the study, all field equipment was battery-operated.

Custom-designed computer programmes, using a software package for signal analysis, Famos 6.2, were used for analysis of EODs. When necessary, EOD duration was corrected to 25 °C using a Q10 value of 1.5 (Kramer and Westby 1985) before data analysis.

The waveform variables of the tetrphasic EOD of *M. anguilloides* were defined as follows (cf. Figure 4a): P1amp, peak amplitude of positive P1 phase (i.e. from baseline to peak, which is equal to $|1|$ V by definition); N0amp and P2amp, negative and positive peak amplitudes of pre- and post-potentials, respectively; N1amp, negative peak amplitude of N1 phase of EOD re: P1amp; N0dur, P1dur and N1dur, durations of respective phases; P1N1sep, separation (or interval) between the peaks of the P1 and N1 phases; and P1area and N1area, areas under the P1 and N1 phases. Total EOD duration was defined as the sum of N0dur, P1dur and N1dur; P2dur was excluded owing to its weak amplitude and slow approach of the baseline in certain discharges, as indicated where appropriate. Durations are given in milliseconds, and amplitudes in relative volts (re: P1-phase amplitude = 1 V). Area-under-curve measures are given in the dimension (volts \times milliseconds). The start of the initial N0 phase was determined at a

threshold level of -2% of P1amp; other phases started and ended between zero-crossings.

The waveform variables of the biphasic EOD of *M. breviceps* were defined as follows (Figure 4b): the head-negative first phase, N, started at -2% of its peak amplitude, Namp, which was $|1|$ V by definition. This was followed by the head-positive second phase, P, that ended at $+2\%$ re: Namp. The other variables were Ndur, Pdur, NPsep, Narea, Parea and EODdur, defined in the same way as described for *M. anguilloides*.

A Fast Fourier transform (FFT) routine, provided by Famos, performed amplitude spectra of single EOD pulses. Analogue-to-digital (A/D) sampling rates of EODs were reduced to between 100 and 125 kHz. The number of data points for FFT analysis was 2^{17} , 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 <2 Hz. The peak power frequency (PPF; in Hz) and the frequencies at -10 dB and -20 dB amplitudes were determined from these spectra.

Subsequent to EOD recording, fish were killed with an overdose of the anaesthetic MS222 or 2-phenoxy-ethanol. SL was measured with vernier callipers or, for specimens longer than 31 cm, a ruler prior to fixing the specimen in 10% formalin for morphological studies.

Material examined

Fish were sampled at the following four stations: (1) the Comoé River at the Campement de Recherche sur les Mouches Tsétsé, Kafolo, Côte d'Ivoire ($9^{\circ}36' N$, $4^{\circ}19' W$), where the river forms the international border between northern Côte d'Ivoire and Burkina Faso; (2) the Bandama River, central Côte d'Ivoire, at the Station d'Écologie de Lamto ($6^{\circ}11' N$, $5^{\circ}0' W$); (3) the Middle Zambezi River in the Batoka Gorge just below the Victoria Falls, on the left bank (Zambian side) of the river at Rapid #6 (about $17^{\circ}56' S$,

25°51' E), and about 800 m above sea level; and (4) the Lower Zambezi River at Tete, Mozambique (16°09'19.3" S, 33°36'01.0" E), on the left bank of the river, at 119 m above sea level (Figure 1).

Mormyrops anguilloides (Linnaeus 1758)

ZSM 42265 (Zoologische Staatssammlung München, the Bavarian State Collection of Zoology), two specimens from the Comoé River, location Kafolo: Kaf014, SL 39.2 cm, male, 18 April 1990, coll. B Kramer and M Postner; Kaf024, SL 45.1 cm, female with ovary egg development stages I–II, 19 April 1990, coll. B Kramer and M Postner.

ZSM 42264, two specimens from the Bandama River, location Lamto: Lam56, SL 27.3 cm, female, ovary stage I, 1 May 1990, coll. B Kramer and M Postner; Lam62, SL 19.2 cm, female, ovary stage I, 1 May 1990, coll. B Kramer and M Postner.

ZSM 42267, two specimens from the Middle Zambezi, Batoka Gorge, Rapid #6: Zam09, SL 18.1 cm, 7 December 1996, coll. FH van der Bank and B Kramer; Zam22, SL 21.2 cm, 8 December 1996, coll. FH van der Bank and B Kramer.

ZSM 42268, one specimen from the Lower Zambezi, location: Tete: R1, SL 21.1 cm, 3 August 2003, coll. FH van der Bank and B Kramer.

Mormyrops breviceps Steindachner 1895

ZSM 42266, two specimens from the Bandama River, location Lamto: Lam11A, SL 39.8 cm, female, ovary weighing 11 g, 20 April 1991, coll. B Kramer and I Kaunzinger; Lam 43A, SL 35 cm, male, 22 April 1991, coll. B Kramer and I Kaunzinger.

Ecology

The Bandama River at Lamto is a perennial river in a region of tropical rain forest, but the water level varies considerably seasonally. Its length is about 950 km (van der Knaap 1994), and the highest water level occurs in September–October (UNESCO, Bandama River at Tiassalé; <http://fr.wikipedia.org/wiki/Bandama>). This is in contrast to the Comoé River at Kafolo, which is an intermittent river, 1 100 km long (<http://www.rezoivoire.net/cotedivoire/patrimoine/105/le-reseau-hydrographique-ivoirien.html#.UTx23zdE-x0>) in dry savanna and fringed by a very narrow gallery forest. The river crosses a typical Sahel zone with scattered small trees. For most of the year, in the dry season, it dries out to a series of pools (*mares*). Paugy's (2002) report on a similar river in Mali, the Baoulé, estimated that in the dry season the series of pools comprises only 10% of its total length, with the lower reaches being completely dry. In the Baoulé, temperature and conductivity reach 35 °C and 120 $\mu\text{S cm}^{-1}$, respectively, and oxygen levels drop to 2.1–3 mg l^{-1} . Fish reproduction in the Baoulé takes place during, or shortly before, a period of intense flooding. Temperature and conductivity fall to 25 °C and 40 $\mu\text{S cm}^{-1}$, respectively. The period of actual flow lasts only 4–5 months (July–November). Much of Paugy's (2002) report on the Baoulé also applies to the Comoé.

Results

Morphology

Bigorne's (2003) key was consulted to identify the present sample of *Mormyrops* specimens from West Africa. Table 1

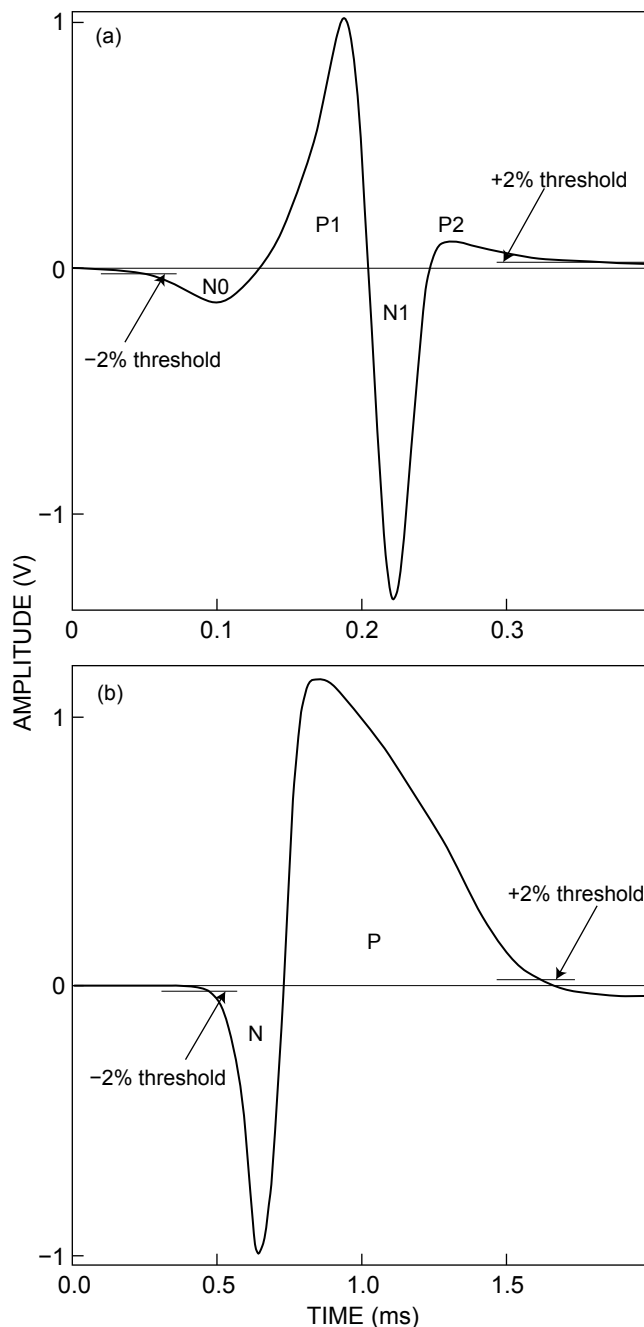


Figure 4: Definition of electric organ discharge (EOD) phases (a) in the tetraphasic EOD of *Mormyrops anguilloides* (specimen field code Lam62) and (b) the biphasic EOD of *M. breviceps* (specimen Lam43A). Both examples are for specimens from the Bandama River. The EOD amplitudes were normalised by their first main phases, which were set to equal 1 V from the baseline (absolute value), i.e. the P1 phase in *M. anguilloides* and the N phase in *M. breviceps*

shows counts and measurements for *M. anguilloides* and *M. breviceps* that can be associated with the present sample.

Four specimens, two from the Comoé River and two from the Bandama River, corresponded well with Bigorne's (2003) data for *M. anguilloides* in West Africa. However, in spite of the wide ranges given, specimen Kaf014 (Comoé

River) was below the range in its caudal peduncle depth (CPD/CPL; 0.322, rather than 0.333, as the lower limit). The other Comoé specimen's CPD/CPL from the same origin (Kaf024) corresponded exactly to the lower limit.

When comparing the present samples of *M. anguilloides* from different origins, considerable differences emerged. Whereas in the Lower Zambezi specimen, R1, the number of lateral line scales (SLS) was above the West African maximum (Bigorne 2003), SLS was just within limits when following Skelton's (2001) definition (Table 1). The three Zambezi specimens' predorsal length (PDL/SL) was consistently greater than the maximum measured in the four Côte d'Ivoire specimens; the same situation pertained to the anal fin ray count (nA), which also exceeded by five rays the value that Linné (1758) reported for the (lost) type specimen. The reverse size relationship held for the length of the dorsal fin (LD/SL) and the distance 'dorsal fin origin to end of caudal peduncle' (pD/SL); their maximum values in the Zambezi specimens were lower than the minimum values in the present sample of Côte d'Ivoire specimens.

The body depth (BD/SL) of the female specimen of *M. breviceps* from the Bandama River was greater than the range for this character given by Bigorne (2003), and the same specimen's number of dorsal fin rays, nD, was lower.

Gosse and Szabo (1960) measured 11 morphological characters in each of their eight *Mormyrops deliciosus* (i.e. *M. anguilloides*) specimens. They concluded that the morphology of the two groups of specimens of different

EOD waveform was so similar that a species difference was unlikely, but suggested the possibility of a sex difference. Gosse and Szabo also highlighted the CPD/CPL data to draw attention to the somewhat higher values in specimens with an initially negative EOD. A statistical significance test between the two groups was, however, not made.

The group difference in Gosse and Szabo's (1960) CPD/CPL data proved significant in both an unpaired *t*-test ($t_6 = -3.098$, $P = 0.0212$) and a Mann-Whitney *U*-test ($U_1 = 0.5$, $U_2 = 15.5$, $Z = -2.191$, $N_1 = N_2 = 4$, $P = 0.0284$). None of the other morphological characters differed significantly between the two groups.

Electric organ discharges

The *M. anguilloides* samples all displayed basically similar EOD waveforms, with a head-positive main phase (P1) followed by a head-negative second main phase (N1) (Figure 5). In addition, all had a weak head-negative pre-potential (N0) and a weak head-positive post-potential (P2). However, in the Comoé specimens, they were so weak that they were difficult to discern at normal amplification. The amplitude of the N1 phase varied among origins; the highest absolute values (re: P1 phase = |1| V) were observed in the Zambezi sample (N1amp = 1.65 V), intermediate values in the Comoé sample (N1amp = 1.5 V), and lowest values in the Bandama sample (N1amp ≤ 1.37 V; Table 2). No polarity-reversed waveforms were seen, including in the specimens from the Comoé River

Table 1: Morphological measurements for samples of *Mormyrops* species from Côte d'Ivoire, Zambia and Mozambique. For abbreviations of morphological characters, see the Materials and methods. Characters taken from Table 15.3 in Bigorne (2003), Skelton (2001) and Linné (1758) are in bold font. Superscript letters indicate measurements or counts for which discrepancies among the present sample of fish were found

Species	PDL/ SL	PAL/ SL	LD/ SL	LA/ SL	LPF/ HL	PPF/ SL	pD/ SL	CPL/ SL	CPD/ CPL	LSc/ HL	LSo/ HL	OD/ HL	IOD/ HL	HL/ SL	HL/ Na	BD/ SL	nD	nA	SPc	SLS	SL (cm)	Sex	
<i>M. anguilloides</i> (from Bigorne 2003)																							
Min.								0.333^a					0.147	0.196		0.133	24	38	12	71			
Max.								0.667					0.345	0.294		0.204	33	50	22	97^b	150		
<i>M. anguilloides</i> (from Linné 1758)																							
																	26	41					
<i>M. anguilloides</i> Comoé River																							
Kaf014	0.647	0.597	0.217	0.317	0.482	0.170	0.358	0.117	0.322 ^a	0.296	0.333	0.073	0.168	0.241	23.29	0.151	27	40	14	80	39.2	M	
Kaf024	0.644	0.584	0.197	0.320	0.489	0.161	0.353 ^b	0.113	0.332	0.294	0.336	0.068	0.189	0.234	23.41	0.180	27	43 ^b	16	77	45.1	F	
<i>M. anguilloides</i> Bandama River																							
Lam56	0.642	0.618	0.204 ^b	0.297	0.480	–	0.362	0.129	0.373	0.293	0.333	0.090	0.148	0.255	24.7	0.173	27	38	15	77	27.31	F	
Lam62	0.657 ^b	0.594	0.203	0.310	0.492	0.159	0.358	0.113	0.394	0.283	0.340	0.107	0.187	0.253	23.23	0.172	28	40	16	75	19.2	F	
<i>M. anguilloides</i> Middle Zambezi																							
Zam09	0.669 ^b	0.568	0.186 ^b	0.369	0.534	0.184	0.323 ^b	0.113	0.385	0.280	0.324	0.094	0.219	0.265	21.95	0.159	–	–	–	80	18.1		
Zam22	0.702	0.581	0.154	0.312	0.564	0.161	0.322	0.118	0.384	0.288	0.332	0.097	0.201	0.27	26.27	0.16	24	46 ^b	16	79	21.2		
<i>M. anguilloides</i> Lower Zambezi																							
R1	0.673 ^b	0.597	0.163 ^b	0.317	0.506	0.167	0.330 ^b	0.114	0.376	0.288	0.334	0.108	0.212	0.245	19.22	0.185	26	46 ^b	18	99 ^b	21.1		
<i>M. anguilloides</i> (from Skelton 2001)																							
Min.																		21	38	85			
Max.																		30	51	100	120		
<i>M. breviceps</i> (from Bigorne 2003)																							
Min.								0.37					0.108	0.161		0.086	27^c	41	12	82			
Max.								0.526					0.2	0.233		0.125^c	33	51	18	109	65		
<i>M. breviceps</i> Bandama River																							
Lam11A	0.649	0.570	0.213	0.337	0.410	0.188	0.361	0.111	0.388	0.277	0.305	0.066	0.133	0.216	28.72	0.139 ^c	25 ^c	43	18	97	39.8	F	
Lam43A	0.650	0.557	0.228	0.314	0.424	0.164	0.385	0.110	0.392	0.271	0.298	0.085	0.130	0.213	28.75	0.119	27	44	16	101	35	M	

^a *M. anguilloides* (West Africa)

^b Comparisons with those from the Zambezi River

^c *M. breviceps*

that were of both sexes. The Comoé specimens, and at least one Bandama specimen, were of a sexually mature size (over 210 mm SL for Côte d'Ivoire; Paugy 2002), and the Comoé male's EOD lasted longer than the female's (0.42 ms vs 0.30 ms). Both P1 and N1 phases of the male contributed to this effect.

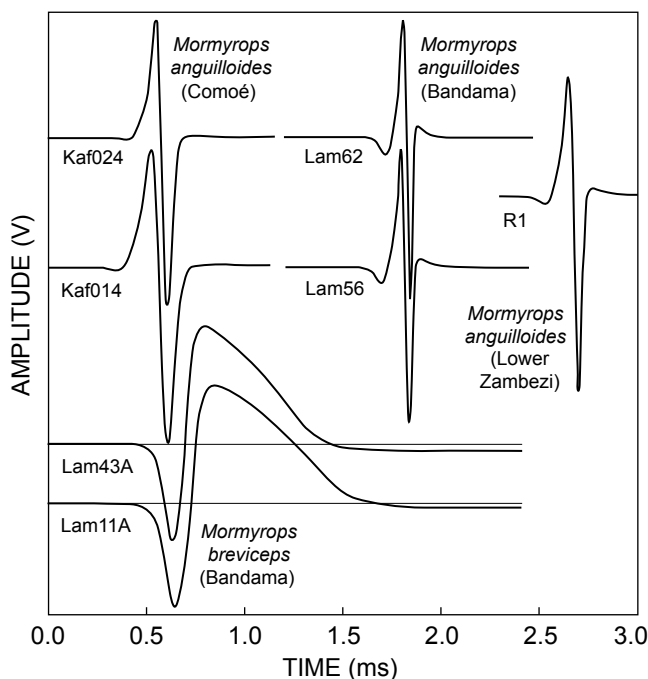


Figure 5: Field recordings of electric organ discharge (EOD) waveforms of all forms or species of *Mormyrops*, with field codes and the rivers they were caught in (in parentheses). Potentials above the baseline are head-positive and those below are head-negative. *Mormyrops breviceps* EODs are shown with the baseline superimposed. Comoé (Kafolo) and Bandama rivers (Lamto) are in Côte d'Ivoire, the Lower Zambezi recording is from Tete, Mozambique. Kaf014 and Kaf024 = *M. anguilloides* (Comoé), Lam56 and Lam62 = *M. anguilloides* (Bandama), R1 = *M. anguilloides* (Lower Zambezi), Lam43A and Lam11A = *M. breviceps* (Bandama)

The Bandama specimens were both females and, in spite of a measurable P2 phase duration that, in contrast to the Comoé EODs, contributed to the duration value of their EODs, the Bandama EODs (0.32–0.33 ms) did not last longer than those of the Comoé specimens. The Zambezi specimen's EOD resembled the Bandama waveform, with pre- and post-potentials >7% re: P1amp, but was of slightly longer duration (0.37 ms). The Bandama EODs had considerably less low-frequency and much greater high-frequency content than the Comoé EODs (Figure 6). The peak power frequencies (PPFs) for the Comoé EODs were $\leq 4\,508$ Hz, compared to $\geq 4\,497$ Hz in the Bandama EODs, whilst the Lower Zambezi specimen's EOD was intermediate (PPF = 5 219 Hz). Accordingly, the -10 dB frequencies were much higher in the Bandama EODs ($\geq 17\,680$ Hz) than in the Comoé EODs ($\leq 11\,560$ Hz), and similarly for the -20 dB frequencies.

Polarity-reversed waveforms, i.e. waveforms with an initially negative main phase, were only seen in the two *M. breviceps* specimens of opposite sex from the Bandama River; both their EODs started with a head-negative main phase followed by a large head-positive P phase of long duration. There was no pre-potential. Pulse duration varied from 0.93 ms to 1.15 ms, and again the longer pulse was displayed by the male. Both fish were of a sexually mature size (≥ 35 cm SL, with maximum species size reported as 65 cm SL; Bigorne 2003). The initial N phase (0.21–0.25 ms) was of short duration, compared to the P phase of longer duration (0.72–0.89 ms) and higher peak amplitude (1.14–1.22 V re: Namp = $|1|$ V). Their amplitude spectra were in the low-frequency range, with PPFs of 392 and 470 Hz and -10 dB frequencies $\leq 3\,040$ Hz on the high-frequency side. On the low-frequency side, attenuation dropped by only 2 dB at 1 Hz, i.e. these EODs had a marked DC component.

Discussion

The morphological data of the four *M. anguilloides* specimens from Côte d'Ivoire, with one exception, were well within the limits given by Bigorne (2003) for the West African form of this species. Of the two specimens from the

Table 2: Electric organ discharge (EOD) waveform characters in *Mormyrops* specimens from the Comoé, Bandama and Lower Zambezi rivers. For abbreviations of the character names see the Materials and methods

Specimen	N0amp (V)	N1amp (V)	P2amp (V)	P1dur (ms)	N1dur (ms)	P1N1sep (ms)	P2dur (ms)	P1area (V × ms)	N1area (V × ms)	N0dur (ms)	EODdur (ms)	SL (cm)	Sex
<i>M. anguilloides</i> Comoé River													
Kaf014	-0.0247	-1.4991	0.0253	0.1848	0.1643	0.0844	–	0.0814	0.1103	0.0688	0.418	39.2	M
Kaf024	-0.0277	-1.4231	0.0264	0.1478	0.1105	0.0593	–	0.0595	0.0744	0.0426	0.3008	45.1	F
<i>M. anguilloides</i> Bandama River													
Lam56	-0.129	-1.315	0.0717	0.0888	0.0531	0.0416	0.0849	0.041	0.0387	0.1069	0.3338	27.3	F
Lam62	-0.152	-1.3745	0.0949	0.0743	0.0423	0.0346	0.0945	0.0354	0.0323	0.105	0.3162	19.2	F
<i>M. anguilloides</i> Lower Zambezi													
R1	-0.0749	-1.6468	0.0727	0.1138	0.0709	0.0537	0.0857	0.0521	0.0619	0.0966	0.367	21.1	
Specimen	P (V)		Pdur (ms)	Ndur (ms)	NPsep (ms)	Parea (V × ms)		Narea (V × ms)		EODdur (ms)	SL (cm)	Sex	
<i>M. breviceps</i> Bandama River													
Lam11A	1.2198		0.7216	0.2096	0.1637	0.4987		0.0961		0.9312	39.8	F	
Lam43A	1.1423		0.8921	0.2546	0.2039	0.5599		0.1168		1.1467	35	M	

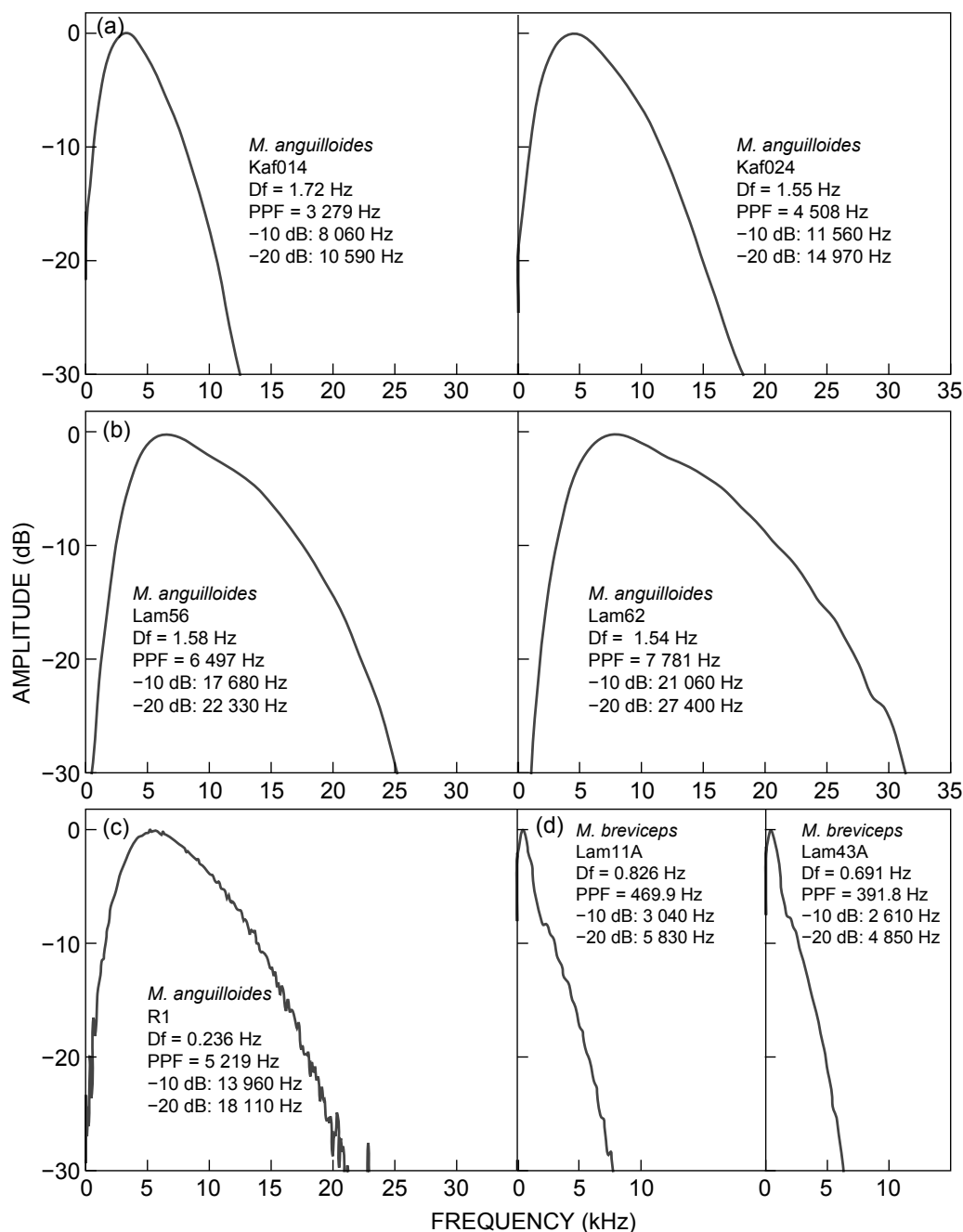


Figure 6: Amplitude spectra of single electric organ discharge (EOD) pulses of *Mormyrops* species. Amplitudes relative to the strongest spectral signal component = 0 dB. The abscissae give the frequency in kHz. (a) Two specimens of *M. anguilloides* from the Comoé River, Côte d'Ivoire, with field code numbers; (b) two specimens of *M. anguilloides* from the Bandama River, Côte d'Ivoire, with field code numbers; (c) *M. anguilloides* from the Lower Zambezi; (d) two *M. breviceps* specimens from the Bandama River, Côte d'Ivoire, with field code numbers. Df = Frequency resolution, PPF = peak power frequency; frequencies at -10 dB and -20 dB re: 0 dB on the high frequency side

Comoé River, but not those from the Bandama River, one had a caudal peduncle only as deep (CPD/CPL), and the other specimen even less deep, than the lower limit given by Bigorne (2003). Bigorne's (1987) definition of *M. anguilloides* includes several nominal species and one subspecies, namely *M. deliciosus* (Leach 1818), *M. longiceps* (Günther 1867), *M. curviceps* Roman 1966, and *M. anguilloides voltae* Roman 1966. Therefore, and because of the

recognition of geographical clines rather than species differences, the ranges given for morphological characters are wide (Bigorne 1987, 2003). The two Comoé samples, with their slender caudal peduncles, are therefore surprising.

Caudal peduncle depth to length ratio is the one variable that Gosse and Szabo (1960) highlighted as potentially betraying a species difference between their eight *Mormyrops* samples, four of polarity- and four of

non-polarity-reversed EODs, a hypothesis they then rejected in favour of a sex difference. They were, however, unable to confirm this since their specimens were of an immature size. As the present paper shows, the two EOD groups (inverted or not) differed significantly in their caudal peduncle depth to length ratios (see Results). The type of caudal peduncle (deep or slender) is correlated with the type of EOD polarity and the type of innervation pattern of electrocytes, as shown by Gosse and Szabo (1960). Together, these correlated observations strongly argue in favour of a species difference, not a sex difference. Caudal peduncle depth and length were identified as the most variable morphological characters among *Mormyrus* samples of several species across Africa, loading principal component 1 most strongly (Kramer 2013a). *Mormyrus* is a genus whose members also tend to be large, and in mormyrids the caudal peduncle holds the electric organ.

Polarity-inverted and non-inverted EODs in members of the same species were not seen in the present study. The two Comoé samples of opposite sex and sexually mature size displayed short, biphasic EOD pulses of 0.3–0.42 ms duration and similar waveform, with an initially positive main phase P1 (the male pulse was of the longer duration). At <3% of the P1 main phase, P1 amplitude, a head-negative pre-potential and a head-positive post-potential were present, but very weak. This is in contrast to the EODs of the two Bandama samples and the Zambezi specimen, which had well-developed pre- and post-potentials (7–15% of P1amp), but were otherwise of similar waveform compared to the Comoé specimens. The only polarity-reversed EODs (with an initially head-negative main phase) seen in the present specimens were those of *M. breviceps*, the two specimens of which were of opposite sex and sexually mature size. The male's and the female's EODs were of the same waveform, and again the male EOD was of longer duration (1.15 rather than 0.93 ms). *Mormyrops breviceps* is morphologically very close to *M. anguilloides* (Bigorne 2003: 187). Could some of the reports of polarity-reversed EODs be due to misidentified *M. breviceps*, or forms of that species, as has happened before (Bigorne 1987)?

A species difference for the *Mormyrops* specimens of Gosse and Szabo (1960) should also not be ruled out when considering other mormyrid genera, several cryptic sibling species of which were discovered by EOD waveform differences. It is true that several mormyrid species exhibit a sex difference in EOD pulse duration, but not pulse polarity as hypothesised by Gosse and Szabo (1960). The most spectacular sex difference known to date was observed in field-studied, sexually mature *Marcusenius altisambesi* Kramer, Skelton, van der Bank and Wink 2007 with an approximately 10-fold increase in male pulse duration during the reproductive season (Kramer 1997b, Kramer et al. 2007). A marked downshift of the amplitude spectrum to low frequencies is associated with this change, putting the males at a high predation risk from certain electroreceptive catfish (Hanika and Kramer 2000). A simple inversion of a pulse waveform, such as that seen in Gosse and Szabo's (1960) fish, however, does not change the amplitude spectrum and is equivalent to a 180° phase shift of its spectral components. Trained, food-rewarded *Pollimyrus*

adpersus (Günther 1866) discriminated playbacks of synthesised versions of artificial EODs, modelled on their species' EOD, that differed only in polarity; the experimental subjects also discriminated much smaller phase shifts than 180° (Paintner and Kramer 2003). This sensory acuity clearly aids in individual recognition of conspecifics by EOD waveform, which was shown in trained, food-rewarded *P. adpersus* and *Gnathonemus petersii* (Günther 1862) (Graff and Kramer 1992).

Cryptic sibling species were first detected by EOD waveform differences that, when investigated, were substantiated by morphological and/or genetic differentiation in the pair *Mormyrus rume* Valenciennes 1846/*M. subundulatus* Roberts 1989 (Crawford and Hopkins 1989, Roberts 1989, Kramer 2013a), the genus *Campylomormyrus* Bleeker 1874 (Feulner et al. 2006), the *Marcusenius macrolepidotus* (Peters 1852) complex (Kramer et al. 2007, Kramer and Wink 2013), the *Marcusenius* species of Côte d'Ivoire (Kramer 2013b), the *Pollimyrus castelnaui* (Boulenger 1911) complex (Kramer et al. 2003, Kramer et al. in press), the *Hippopotamyrus ansorgii* (Boulenger 1905) complex (Kramer et al. 2004, Kramer and Swartz 2010), the *Petrocephalus catostoma* (Günther 1866) complex (Kramer and van der Bank 2000, Kramer et al. 2012), and the pair *Cyphomyrus discorhynchus* (Peters 1852) and *C. angolensis* (Pellegriin 1936) (Kramer and van der Bank 2011). Similar observations, with some overlap of EOD characteristics, were made in the sibling species pair *Ivindomyrus opdenboschi* Taverne et Géry 1975 and *I. marchei* Sauvage 1879 (Lavoué et al. 2008a), and a rich EOD waveform variation was revealed in the genus *Paramormyrops* Taverne, Thys van den Audenaerde and Heymer 1977 (Sullivan et al. 2004).

Radically different EOD waveform shapes among species within a genus have been observed previously, for example, in *Mormyrus* (Kramer 2013a), *Hippopotamyrus* (Kramer and Swartz 2010), and *Pollimyrus* (Kramer et al. 2003). These are in contrast to mormyrid genera such as *Marcusenius* or *Petrocephalus*, whose members form a family of basically similar EOD waveforms that are only moderately varied among species (Kramer et al. 2007, Lavoué et al. 2008b, Kramer et al. 2012). Hence, a distant relationship between two mormyrid species cannot automatically be inferred from dissimilar EOD waveforms. Radical differences in the EODs among closely related species are, therefore, not unheard of amongst mormyrids. However, polarity inversion in the members of one and the same species, as suggested for *M. anguilloides*, is unproven to date. On the basis of all the evidence available, it is concluded that the reports of both polarity-inverted and non-inverted EOD waveforms in *M. anguilloides* most probably indicate the presence of an unrecognised species.

In addition to caudal peduncle depth, the Comoé and Bandama specimens of *M. anguilloides* showed substantial differentiation in EOD waveform and amplitude spectra. The EODs of the former specimens were essentially biphasic, relatively low-frequency pulses (with only weak pre- and post-potentials) compared to the latter, which were clearly tetraphasic, high-frequency pulses. The specimens from the two rivers also seemed to differ in N1 phase amplitudes, N1amp, which were higher in the Comoé

specimens. This calls for clarification of their systematic relationship in future studies.

The Comoé River specimens at Kafolo live in a much harsher dry savanna environment than those of the Bandama River at Lamto in their lush tropical rainforest environment. In their intermittent river habitat, the Comoé specimens undergo a seasonal, drastic reduction of habitat volume, as well as heat and oxygen stress, compared to those in the perennial Bandama River. This difference certainly has consequences for life history and reproduction, as discussed by Paugy (2002) for the Baoulé River, which is of similar ecology, and may be connected to the differentiation observed.

The type locality of *Mormyrops breviceps* is Liberia ('aus dem St Paul-Flusse'; Gosse 1984). Linné (1758: 327) gives 'Habitat in Nilo' (lives in the Nile River) as the type locality for *M. anguilloides*, the type specimen of which has been lost (Gosse 1984). The differentiation observed among the present Côte d'Ivoire and Zambezi *M. anguilloides* specimens (Tables 1 and 2) points to the existence of undiscovered species differences across Africa that have yet to be substantiated by the critical comparison of local populations with the type material. Therefore, a neotype for *M. anguilloides* from a local population of Nile specimens is needed, chosen from a location that would have been accessible to Linné or his fish provider, unless the exact type locality can be ascertained from historical records. Only when the definition is narrowed down to characterise the type population, or one that takes its place, which is not so wide that it embraces specimens from almost the whole of Africa, will it become possible to construct the phylogeography of local populations across Africa.

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