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# Meristic Characters and Electric Organ Discharge of Mormyrops curviceps Roman (Teleostei: Mormyridae) from the Moa River, Sierra Leone, West Africa

# PETER MOLLER AND BARBARA BROWN

Mormyrids of the genus *Mormyrops* were collected from the Moa River around Tiwai Id., Sierra Leone, West Africa. Meristic analysis and comparison with paratypes identify these fish as *Mormyrops curviceps* Roman. They differ from *M. deliciosus* (Roman) in seven meristic characters: the number of lateral-line scales, caudal-peduncle scales, total vertebrae, caudal vertebrae, anal-fin rays, and teeth on the upper and lower jaws. From *M. curviceps* we recorded two electric organ discharge (EOD) pulse types, which were not related to developmental stage or sex. Individual EOD lasted on average either 0.471 msec (with a major head-positive phase followed by an equally large head-negative phase), or about three times longer (1.611 msec) with reversed polarity (i.e., a major head-negative phase), followed by a major head-positive phase. We contrast two views concerning mormyrid EOD: 1) the EOD of *M. curviceps* simply exists in two pulseform morphs; and 2) characteristics of the EOD pulse-form function as a reproductive isolating mechanism, suggesting the existence of sibling species.

MORMYRIDS are prominent in the fish fauna of the Taia and Moa rivers in Sierra Leone, surveyed by staff of the Department of Zoology, Njala University College of the University of Sierra Leone. Several species of the genus Mormyrops (among them Mormyrops endoloti), constitute an important dietary protein supplement for local human populations. In 1986 and 1987 we conducted an eco-ethological survey of the electric fish fauna in the Moa River (Cain et al., unpubl.). Preliminary meristic data from specimens of Mormyrops were incongruent with assignment to M. deliciosus, a species previously believed to occur in the Moa River. We also found subtle differences in the pulse form of the fish's electric organ discharge (EOD) that were not related to sex or developmental stage. We were interested in whether the Moa River Mormyrops belong to different species or represent two pulse-form morphs of one species. In this study we compared our material with two species within the genus Mormyrops: M. deliciosus Leach (1818) and M. curviceps Roman (1966).

## MATERIAL AND METHODS

Study site and collecting methods.—Tiwai Id. (7°33'N, 11°21'W) is the largest island (12 sq. km) in the Moa River, one of the largest rivers on the eastern side of Sierra Leone. It is in Barri Chiefdom, Pujehun District, about 60 km inland from the Atlantic Ocean, close to the western edge of the Gola West Forest Reserve. Tiwai has no permanent human settlement, and represents in microcosm the main features of the Upper Guinea forest. The climate is tropical with air temperatures reaching 29 C in the rainy season (May-Oct.) and 40 C in the dry season (mid-Nov.-mid-March). Fishes were caught, with the help of local laborers from Kambama village on the mainland, during the night with gill nets (mesh width 2.5 cm) and hook and line. Fishes were collected during two trips, one during the dry season in Jan. 1986 (18 specimens, AMNH 77360) and a second during the wet season in June-July 1987 (six specimens, AMNH 79250; 10 specimens, AMNH 79251). Institutional abbreviations are as listed in Leviton et al. (1985).

EOD recordings.—Fish were caught during the night and brought to camp before daybreak. When they were alive and in good condition, they were transferred into large plastic holding containers filled with river water. Individual fish were subsequently placed into a smaller recording tank ( $30 \times 30 \times 25$  cm high) fitted with a pair of Ag/AgCl electrodes in diagonally opposing corners. Electric organ discharges were recorded while the fish faced the positive electrode, and displayed directly, unamplified, on the screen of a Tektronix 455 portable dual trace oscilloscope powered by a 12 V car battery

(input impedance 1 MOhm, capacitance 20 pF). The fish's EOD were triggered on one trace using the oscilloscope's highest sensitivity (5 mV/div) and displayed in parallel on the second trace adjusting the peak-to-peak amplitude to fill a full screen. The duration of the individual EOD and its phases were read directly from the oscilloscope using the zero crossings of the EOD from the high-sensitivity input as references. Electric organ discharges were photographed with a Tektronix Polaroid camera (C-30A). Comparisons of EOD recorded in this manner with EOD monitored from undisturbed fish using probing electrodes showed no detectable differences in pulse form.

Water temperature and conductivity in the recording tank ranged from 22.5–27.5 C and 50–80  $\mu$ S/cm, respectively. Each fish was measured (standard length to nearest mm, and fresh weight to nearest g), photographed and subsequently killed. Sex was determined by inspection of the gonads. The fish were preserved in formalin and prepared for transport to our laboratory at the American Museum of Natural History.

Species identification.—We measured all Tiwai Id. specimens with a pair of dividers and counted lateral-line scales, caudal-peduncle scales and teeth. All other counts were made from radiographs. Fin-ray counts include both branched and unbranched rays of the dorsal and anal fins. Whenever possible (some of the AMNH specimens are quite old), we determined the number of lateral-line scales, and upper- and lower-jaw teeth for *M. deliciosus* specimens from the AMNH collection. In addition, ranges of lateral-line scale and tooth counts for *M. deliciosus* and *M. curviceps* were taken from Roman (1966).

We examined three paratypes of *M. curviceps* on loan from the MRAC collected in the Upper Volta, and 34 specimens of *M. deliciosus* from AMNH, all from the Zaire (Congo) River (see Material Examined).

Statistical analysis.—Mean meristic values and morphometric measures were compared using a (two-tailed) Student's t-test. Regression analyses were conducted to test the relationship between size of the fish and the various taxonomic measures. Levels of confidence are indicated in the text.

## RESULTS

Meristic comparisons.—Nine meristic criteria (A-I in Fig. 1) were used to compare our specimens with the museum material and published data for these species (Roman, 1966): number of lateral-line scales, total vertebrae, caudal and abdominal vertebrae, predorsal bones, dorsal- and anal-fin rays, and upper- and lower-jaw teeth. First, we compared the Tiwai specimens collected during two trips in 1986 and 1987. Both Tiwai samples were then combined and compared as a group with *M. deliciosus* (AMNH and Roman, 1966). Finally, we compared the Tiwai fish with the paratypes of *M. curviceps*.

Tiwai 1986 vs Tiwai 1987.—There was no difference between the two samples with the exception of anal- and dorsal-fin rays (Fig. 1F–G). Since the mean of the combined distributions for anal-fin rays differed significantly from that of *M. deliciosus* (Fig. 1F), but not from that of *M. curviceps*, we felt justified to combine the two Tiwai samples. The dorsal-fin ray count for the combined Tiwai sample was not different from that of *M. deliciosus* (Fig. 1H).

Tiwai vs M. deliciosus.—Tiwai and M. deliciosus specimens differed significantly in six characters: number of lateral-line scales, total vertebrae, caudal vertebrae, anal fin rays, and upper and lower teeth (Fig. 1A–C, 1F, 1H–I). The respective ranges of number of lateral-line scales, and upper- and lower-jaw teeth for Tiwai specimens fell within those reported for M. curviceps by Roman (1966). Counts of abdominal vertebrae, dorsal-fin rays, and predorsal bones overlapped in the two groups and were not significantly different (Fig. 1D–E, 1G).

Tiwai vs M. curviceps.—We compared the six meristics in which the Tiwai specimens differed from M. deliciosus with the data from the three paratypes of M. curviceps. There was no significant difference between the two groups (Fig. 1), and we concluded that the Tiwai specimens best fitted the description for M. curviceps.

Morphometric data on the Tiwai M. curviceps.—We measured SL and fresh weight in the field. In addition to the nine meristics described above, we also investigated the following 10 measures obtained from fixed specimens upon return to our laboratory at the AMNH: A) anal-fin length; B) head length; C) dorsal-fin length; D) body depth; E) head depth; F) length of caudal peduncle; G) number of ribs, H) number of epiplural ribs; I) depth of caudal peduncle; and J) number of caudal-peduncle scales (Fig. 3A–B). Whenever possible, these measurements were compared with those from the three paratypes.



Fig. 1. Comparison of *Mormyrops curviceps* (TW 86 and TW 87 = specimens collected in Jan. 1986 and in June–July 1987 at the same site around Tiwai Id. in the Moa River, Sierra Leone; TW 86/87 = combined data; P = paratypes of *M. curviceps*; C\* = range data from Roman, 1966) and *M. deliciosus* (D = AMNH specimens; D\* = range data from Roman, 1966) on nine morphometrics (A–I). Length of open bar = range; dot inside bar and vertical line = mean  $\pm 1$  SD; number on top of open bar = sample size; statistical comparisons: open triangle = not significant, black triangle = significant (P < 0.001).



Fig. 2. Relationship between SL and weight in *Mormyrops curviceps*. s =short EOD pulse type, l =long EOD pulse type. Identification (AMNH) is given next to symbols and refers to specimens whose EOD are illustrated in Figure 4. W = fresh weight in g, L = standard length in mm.

Length-weight relationship.—The relationship between SL and weight is illustrated in Figure 2. The highest coefficient of determination ( $r^2 = 0.974$ ) was obtained when the data were subjected to a power regression analysis. Thus, the length-weight relationship is best expressed as a power function in the form of W = aL<sup>b</sup> × 10<sup>-5</sup> (W, fresh weight in g; L, standard length in mm; and two empirically determined constants, a = 5.17 and b = 2.59).

Morphometrics and additional meristics. — Depending on the preserved condition of the fish, data (characters A–J, see above) were obtained from 12–18 specimens that ranged in size from 169–315 mm SL. Clearly, characters A–E are positively correlated with SL (Fig. 3A). The coefficient of determination ( $r^2$ ) for these five measures exceeded 0.95. The dependence of these measures on size excluded them from use in species identification.

The correlation of the caudal peduncle measures F and I with SL was significant, but characterized by a slow-rising slope (Fig. 3B). The coefficient of determination for these two measures was 0.67 and 0.54, respectively. Measures G-H and J were independent of SL (Fig. 3B). Thus, the number of ribs, epiplural ribs, and caudal-peduncle scales can be used as size-independent species characters. We used these three criteria and compared AMNH specimens of M. deliciosus with M. curviceps collected around Tiwai Id. The number of caudal-peduncle scales differed significantly between the two species (Student's t-test: P < 0.001; t = 13.45, df = 46; *M. deliciosus*, range: 15-19, mean:  $17.7 \pm 1.1$ , n = 31; and M. curviceps, range: 12–14, mean:  $13.8 \pm 0.6$ , n = 17). The number of epiplural ribs was significantly different between the two species (P < 0.05; t = 2.31, df = 45). There was no difference in the total number of ribs.

Our data suggest that, in addition to the six meristic characters described above, the number of caudal-peduncle scales can be used to distinguish between *M. deliciosus* and *M. curviceps*.

Comparison of Tiwai vs Paratypes.—For all 10 measures we calculated the best-fitting linear functions (regression equations) expressing the



Fig. 3. Correlations between SL and 10 different measures for *Mormyrops curviceps*. P next to symbol indicates measure from paratype. A) Measures A–E depended on SL of fish; B) measures G–J were independent of the fish's size, but only J (number of caudal peduncle scales) was a useful meristic to distinguish between *M. curviceps* and *M. deliciosus*.

relationship between the individual measure and SL. The corresponding measures obtained from the three paratypes of M. curviceps (Fig. 3A–B; 139, 175, 222 mm SL) fell within the 95% confidence limits calculated for the regression equations.

Electric organ discharges.—We were able to record EOD from 16 Tiwai specimens and could assign them to two pulse types (Fig. 4). Short pulses (11 fish) lasted on average 0.471 msec and consisted of four phases: a small head-negative phase (mean duration and SD: 0.137  $\pm$ 0.006 msec), followed by a major head-positive phase (0.138  $\pm$  0.046 msec), an equally large head-negative phase (0.138  $\pm$  0.052 msec), followed by a small fourth head-positive phase (0.156  $\pm$  0.039 msec). Long pulses (five fish) lasted on average 1.611 msec and consisted of two clearly detectible phases: a major head-negative phase (0.218  $\pm$  0.035 msec), followed by a large head-positive phase (1.135  $\pm$  0.176 msec).

Adult females (Fig. 5; AMNH 77360.03, and 77360.06) that were of comparable SL (315, 327 mm), and also contained eggs of comparable size (about 1 mm in diameter) emitted either short or long pulses. Both pulse types were also found in immature fish for which the sex could not be determined (Fig. 2). Our data did not allow an assignment of the two pulse types to either developmental stage or sex of AMNH 77360



Fig. 4. Two electric organ discharge morphs recorded from *Mormyrops curviceps*: long biphasic discharges (left) lasting on average 1.611 msec, and short discharges (right), characterized by four phases, lasting on average 0.471 msec. Specimens are catalogued (AMNH 77360) and individually identified (.01-.06); m = male, f = female; p-t-p = peak-to-peak amplitudeof the EOD is indicated alongside panels. Note difference in EOD amplitude between the two EODmorphs under identical recording conditions.

*M. curviceps.* The peak-to-peak amplitude of the EOD, determined under identical recording conditions, was significantly larger in fish emitting long pulses than in fish emitting short pulses (Fig. 4).

### DISCUSSION

The holotype (255 mm) and nine paratypes (141–226 mm) of *M. curviceps* were collected in 1964 in the Bougouriba, a tributary of the Black Volta River. The assignment of the specimens from the Bougouriba and Black Volta (one additional specimen, 430 mm) to a new species (Roman, 1966) was based on a comparison with *M. deliciosus* collected in the Upper Zaire (Congo) River, north of Angola. The *M. curviceps* population was characterized by having a smaller number of teeth and lateral-line scales. Roman (1966) compared adult specimens from

both species and distinguished between the two on the basis of their head shape: "the head is more elongate and compressed in M. curviceps than in M. deliciosus." Roman (1966) assumed that M. deliciosus was absent from the Upper Volta River. Although our sample sizes are small (1986, n = 18; 1987, n = 16), we emphasize that all specimens are M. curviceps, which indicates that M. deliciosus is probably also absent from the Moa River. Thus, to date, M. curviceps has been reported only from the type locality in the Upper Black Volta River and our collection site in the Moa River. Daget et al. (1984) listed the distribution of *M. deliciosus*, whose type locality is the Zaire River, as Senegal; the Gambia, Niger, Chad, Zaire, Volta and Zambesi basins; lakes Malawi and Tanganyika; and Whebi Shebeli and Juba (Samalialand). We found M. deliciosus also in Lake Kainji, Nigeria (Moller et al., 1979). In a recent revision of the genus Mormyrops, Bigorne (1987) suggested that variations observed in M. curviceps and M. deliciosus resulted from geographic gradients rather than true specific differences, and classified them together with three other congeneric species as M. anguilloides (Linnaeus, 1758).

Sympatric adult *M. curviceps* emitted two distinctly different, individual-related EOD pulse forms. Individual fish were never observed to emit both types of discharges. It seems unlikely, taking into account neural and hormonal control mechanisms (Bass, 1986a, 1986b; Freedman et al., 1989) that individual fish could switch within a short time between discharges of such dramatic difference as that observed in *M. curviceps*. Short-term, stress-related conditions, on the other hand, can result in minor, but significant changes in EOD pulse form (Landsman, 1990; Landsman et al., 1987).

The intraspecific variability in EOD pulse form was surprising since the two EOD morphs did not reflect a sexual dimorphism, as described for a number of mormyrid species (e.g., *Brienomyrus brachyistius*, long biphasic and triphasic, Hopkins, 1980; *Stomatorhinus walkeri*, Moller, 1980; *Pollimyrus isidori*, Lücker and Kramer, 1981; *Gnathonemus petersii*, Landsman, 1990), and also contrasted with the assumption that *Mormyrops* species were characterized by a head-negative EOD (Bennett, 1971; *M. zanclirostris*: Moller, 1980; Hopkins, 1981).

With the exception of a few published EOD recordings of *M. deliciosus* (Gosse and Szabo, 1960; Bennett, 1971) there exists no systematic study on the EOD pulse form for this species as



Fig. 5. Voucher specimens of *Mormyrops curviceps* (females) collected around Tiwai Id., in the Moa River, Sierra Leone. AMNH 77360.03 = short pulse-form morph, AMNH 77360.06 = long pulse-form morph.

related to developmental stage or sex. A direct comparison of this character between M. deliciosus and M. curviceps is thus not possible. In the field (Zaire River), Gosse and Szabo (1960) recorded EOD from juvenile M. deliciosus (95-140 mm) and found two types of pulse forms that were exact mirror images of each other. The discharge was essentially biphasic, about 1.5 msec in duration, and started with either a large head-negative phase followed by an equally large head-positive phase, or just the opposite. Amplitude and duration of both phases were nearly identical. Gosse and Szabo (1960) examined the morphology of the electric organ and explained the existence of the two pulse types on the basis of the innervation of the electrocytes. The initial head-negative EOD occurs in fish in which the innervation is on the posterior side, whereas the initial head-positive EOD occurs in specimens where the innervation is on the anterior side.

Since Lissmann's (1958) discovery of electroreception in weakly electric fishes, we have learned extensively how these animals use their EOD in orientation and social communication. As a rule, EOD in mormyrids are considered species-specific (Bennett, 1971; Moller et al., 1979; Hopkins, 1980), and may play a role in species isolation as suggested by Hopkins and Bass (1981) for the Ivindo River (Gabon) mormyrid Brienomyrus brachyistius. Individuals among this group did not differ in traditional diagnostic characters (except in anatomical features of the electric organ), but exhibited six different, individual-related EOD: monophasic, biphasic, long biphasic or triphasic pulse forms with an additional sexual dimorphism in pulse form present among long biphasic and triphasic fish (Hopkins, 1980, 1986; Hopkins and Bass, 1981). The authors proposed that EOD characters could assist in species diagnosis. Adhering to a biological species definition, we could assume with Hopkins (1981) that the observed two different EOD pulse forms in M. curviceps are species-specific "fingerprints," and act as a communication barrier between members of the two groups. Accordingly, the Tiwai Mormyrops population would consist of two sibling species. Similarly, in a long-term laboratory study, we found two types of individual-related EOD pulse forms that were not related to sex or developmental stage in the mormyrid Campylomormyrus rhynchophorus, identified on the basis of traditional characters (Moller et al., unpubl.).

The species isolation hypothesis is compelling and should be followed up and supported by appropriate breeding experiments. Until such empirical evidence is available, and traditional diagnostic criteria do not suggest otherwise, we propose calling the different pulse forms EOD morphs. As has been pointed out, polymorphic EOD can reflect a sexual dimorphism in several species, and may indeed indicate the existence of sibling species in the *B. brachyistius* group.

Communication signals serving in species isolation must be highly stereotyped and speciesspecific. Does the mormyrid EOD meet these criteria, and as a potential taxonomic tool, is it as rigid and invariable as morphological characters are? During early development the larval EOD is replaced by an adult signal (Kirschbaum, 1975), whereby specific ontogenetic influences on shape and form of the EOD have not been systematically investigated. In several species the adult signal undergoes maturational changes with the shorter female EOD resembling the juvenile EOD and the male EOD changing its pulse form and increasing in duration (Hopkins, 1980, 1981; Bass and Hopkins, 1985). Such sex differences, however, have been elusive under laboratory conditions unless immediately recorded from freshly imported fish (Landsman, 1990) or induced by hormone treatment (Bass and Hopkins, 1985; Bass, 1986a, 1986b). The sexual dimorphism in the EOD pulse form in Pollimyrus isidori, showing overlap between the sexes, has been reduced to a statistical difference (Westby and Kirschbaum, 1982; Bratton and Kramer, 1988). For Gnathonemus petersii there are data claiming no sex difference in EOD pulse form (Kramer and Westby, 1985), a "reversed sex difference" (Landsman et al., 1987), and finally a natural sex difference with male EOD lasting longer than female EOD (Landsman, 1990). Stress-related conditions can result in minor, but significant, rapid changes in EOD pulse form (Landsman, 1990; Landsman et al., 1987). Such rapid changes are also well documented in a gymnotid fish, Hypopomus, whose EOD at the night of spawning was about twice as long as measured 6 d later (Kawasaki and Heiligenberg, 1989). Comparing the individual EOD of two male M. curviceps (Fig. 4; AMNH 77360.01, 77360.02), we noted a longer lasting phase in the larger male (SL 222 vs 333 mm SL). It remains to be shown whether or not higher testosterone levels were responsible for this difference (Landsman, 1990). Thus, EOD for species diagnosis should preferably be collected from adult specimens under natural conditions during breeding conditions to avoid stress and to rule out confounding maturational and seasonal changes.

The EOD pulse form is affected by changes in aquatic conductivity (Squire and Moller, 1982; Bratton and Kramer, 1988); thus, "EOD data without conductivity data are not very useful" (Crawford and Hopkins, 1989). For EOD to serve as a taxonomic tool, it is important to know the seasonal variations in conductivity in the fishes' habitat and the specific effects on EOD pulse form. In addition to variability in EOD pulse form due to developmental, maturational, and environmental factors, recording methods may also affect EOD characteristics, and comparison of data from authors using different methods could cause confusion (Crawford and Hopkins, 1989).

The evidence for social electric communica-

tion in mormyrid fishes has been inferred from playback experiments (Hopkins and Bass, 1981; Crawford, 1989; Bratton and Kramer, 1989) and controlled dyadic interaction experiments (Crawford, 1989; Moller et al., 1989) by evaluating correlations between sender and receiver EOD activity, or sender EOD activity and receiver locomotor activity: EOD "rasps" and courtship displays in B. brachyistius, for example (Hopkins and Bass, 1981). EOD rasps, however, are not an EOD display specific to B. brachyistius, but can also be recorded from G. petersii and C. rhynchophorus in non-breeding conditions (Moller et al., unpubl.). While these results have shed some light on the specificity and information content of the individual signal and its temporal organization, we also know that in interspecific encounters, fishes emitting EOD that vary considerably in pulse duration and polarity are at least able to attract one another (Moller and Serrier, 1986), and also affect changes in one another's EOD activity: the fishes are not necessarily 'blind' to foreign EOD (Moller and Miller, unpubl.). Such interspecific responsiveness does not rule out species recognition, and may be merely a function of the tuning spectrum of the fish's electroreceptors. However, if EOD are to be used as a taxonomic character in species identification, it is necessary to carefully examine and analyze the EOD characteristics that mormyrid fishes use to recognize potential mates and members of their own species, and to distinguish them from cogeners. Such examination should include, for any given species, an evaluation of the EOD stability and plasticity over time; an account of the range of EOD pulseform variability as affected by developmental, maturational, and environmental factors; behavioral studies to explore individual signal and pattern recognition; and finally, but possibly most difficult to carry out, well-controlled breeding experiments. Results from such a comprehensive examination could suggest that the fish's EOD signature did not reflect a polymorphic trait, but in fact represented a communication barrier, and thus a reproductive isolating mechanism.

#### MATERIAL EXAMINED

Mormyrops curviceps: Paratypes, RGMRAC 140935-140943, 3, 139-222 mm. Mormyrops curviceps: AMNH 77360, 18, 169-315 mm; AMNH 79250, 6, 137-350 mm; AMNH 79251, 10, 126-348 mm. Mormyrops deliciosus: AMNH 6652 (Zaire: Provence Orientale; Faradge Ubangi River), 2, 212-438 mm; AMNH 6718 (Zaire: Provence Orientale; Stanleyville, Zaire River), 2, 102.5-108 mm; AMNH 6730 (Zaire: Provence Orientale; Rungu), 199 mm; AMNH 6747 (Zaire: Provence Orientale; River), 29 Stanleyville, Zaire River), 189 mm; AMNH 6777 (Zaire: Provence Orientale; Faradge Ubangi River), 2, 238–294 mm; AMNH 6818 (Zaire: Provence Orientale; Avakubi, Ituri River), 189 mm; AMNH 6818 (Zaire: Provence Orientale; Avakubi, Ituri River), 189 mm; AMNH 6892 (Upper Zaire River), 2, 71.5–82 mm; AMNH 6878 (Zaire: Provence Orientale; Avakubi, Ituri River), 113 mm; AMNH 6892 (Zaire: Provence Orientale; Stanleyville, Zaire River), 13, 54–151 mm; AMNH 6903 (Zaire: Provence Orientale; Faradge Ubangi River), 7, 66–142 mm; AMNH 12401 (Kasai District; Kasai River), 125 mm; AMNH 19672 (Zaire: Provence Orientale; Mbonu River), 133.5 mm. Mormyrops deliciosus was first described on the basis of specimens from the Zaire (Congo) River (Leach, 1818). All specimens of M. deliciosus used in this study were collected from the Ubangi-Zaire River drainage system and were identified using keys by Boulenger (1909–1916), Roman (1966), and Taverne (1972).

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