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Rediscovery and description of *Paramormyrops sphekodes* (Sauvage, 1879) and a new cryptic *Paramormyrops* (Mormyridae: Osteoglossiformes) from the Ogooué River of Gabon using morphometrics, DNA sequencing and electrophysiology

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Species of the African electric fish in the genus *Paramormyrops* Taverne, Thys van den Audenaerde & Heymer, 1977 constitute a recently recognized species flock with an impressive diversity of electric signals, but only modest morphological differentiation. For more than a century, confusion has surrounded the identity of *Paramormyrops sphekodes* (Sauvage, 1879), the earliest described species in this genus. Here we compare the morphometrics of type material to new specimens collected at the type locality on the Ogooué River of Gabon from which we additionally study DNA sequences and electric organ discharges (EODs). Based on our findings, we revise the diagnosis and description of *P. sphekodes* and also identify and describe a new species of *Paramormyrops* that is large, common and widespread in the Ogooué River basin, but cryptic and easily confounded with *P. sphekodes*. We designate as lectotype of *P. sphekodes* a specimen formerly regarded, in error, as the holotype and a second specimen originally collected with the lectotype as paralectotype. We conclude that only nine additional specimens can be identified with confidence as *P. sphekodes*: four from the type locality and five from a second site 45 km away. Instead of being widespread as previously thought, *P. sphekodes* may be restricted to a small region of the upper Ogooué River basin. Additionally, we present a revised diagnosis for the genus *Paramormyrops* Taverne *et al.*, 1977, and key to species from Lower Guinea. This study illustrates the value of vouchered EOD recordings and of revisiting type localities, and lays a foundation for additional systematic work on this group.

ADDITIONAL KEYWORDS: cryptic species – Cytochrome *b* (cyt-*b*) – electric fish – electric organ discharge (EOD) – Mormyridae – Osteoglossomorpha – *Paramormyrops* – species flock – systematics – taxonomy.

INTRODUCTION

This study focuses on mormyrid weakly electric fishes (Mormyridae: Osteoglossomorpha) in the genus *Paramormyrops* Taverne, Thys van den Audenaerde and Heymer, 1977, notable for their species diversity in the Ogooué River of Gabon and neighbouring river basins in the Lower Guinea Ichthyofaunal Province of West-Central Africa (Roberts, 1975; Stiassny, Teugels & Hopkins, 2007). *Paramormyrops* species exhibit surprisingly diverse electric organ discharges (EODs) but only modest morphological differentiation (Sullivan, Lavoué & Hopkins, 2002; Arnegard & Hopkins, 2003; Arnegard *et al.*, 2010b). EOD pulses are often species-specific and play a significant role in reproductive isolation (Hopkins & Bass, 1981). Increasingly, EODs have been used in mormyrid systematics (Sullivan & Hopkins, 2004; Hopkins, Lavoué & Sullivan, 2007; Lavoué, Sullivan & Arnegard, 2010; Kramer, Van der Bank & Wink, 2014; Lavoué & Sullivan, 2014). Here

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we clarify the identity of the earliest described species now placed in this genus, *Paramormyrops sphekodes* (Sauvage, 1879), by comparing type material to specimens newly collected at its type locality, combined with study of EODs and DNA sequences.

Family Mormyridae and genus *Paramormyrops*

There are currently 228 recognized mormyrid species placed in 21 genera (Eschmeyer, 2015; Sullivan & Lavoué, 2016; Sullivan, Lavoué & Hopkins, 2016), all of which produce low-voltage EODs in a muscle-derived electric organ in the caudal peduncle. They sense their own EODs as well as those from other individuals using specialized tuberous electroreceptors distributed over the skin surface (Fessard & Szabo, 1961; Bennett, 1965, 1971; Bass, 1986). These specialized structures serve in two essential functions: electrolocation of objects (Lissmann & Machin, 1958; von der Emde *et al.*, 2008; Hofmann *et al.*, 2013) and intraspecific electrical communication (Möhres, 1957; Moller, 1970, 1995; Moller & Bauer, 1973; Bell, Myers & Russell, 1974; Kramer, 1974; Hopkins & Bass, 1981; Hopkins, 2009), facilitating activity at night or in murky water.

The genus *Paramormyrops* was established by Taverne *et al.* (1977) with *Paramormyrops gabonensis* designated as the type species. The genus was enlarged by Hopkins *et al.* (2007) who reclassified as *Paramormyrops* six species from Lower Guinea that Taverne (1972) had placed into three other genera: *Brienomyrus* Taverne, *Pollimyrus* Taverne and *Hippopotamyrus* Pappenheim (see Systematics section). The impetus for this reclassification was a series of molecular phylogenetic studies using both mitochondrial and nuclear markers (Alves-Gomes & Hopkins, 1997; Lavoué *et al.*, 2000; Sullivan, Lavoué & Hopkins, 2000; Sullivan *et al.*, 2002, 2004) that consistently identified a monophyletic group consisting of *P. gabonensis*, five species placed in other genera and as many as 16 undescribed taxa from the Ogooué River and neighbouring watersheds. On the phylogenetic tree of Mormyridae this clade is not closely related to the type species of *Brienomyrus*, *Pollimyrus* or *Hippopotamyrus*, but is instead the sister-lineage of *Marcusenius ntemensis* (Pellegrin, 1927). This latter species from the Ntem and Ivindo Rivers is itself in need of taxonomic revision as molecular phylogenetics show that it is not closely related to other *Marcusenius* species (Lavoué, Sullivan & Hopkins, 2003).

Sullivan *et al.* (2002, 2004) first identified this clade (originally referred to as 'Gabon-clade *Brienomyrus*' because most of the species were then classified in the genus *Brienomyrus*) as a 'riverine species flock' in the Ogooué basin of Gabon, parallel in some ways to that seen within another mormyrid genus – *Campylomormyrus* – in the lower Congo River (Feulner *et al.*, 2007). The high proportion of sympatric species with distinctive EOD waveforms within both genera suggests that electric signals may have evolved as reproductive isolating mechanisms accompanying ecological differentiation (Feulner, Kirschbaum & Tiedemann, 2008; Feulner *et al.*, 2009) or that sexual selection on EOD features may drive the speciation process (Arnegard *et al.*, 2010a).

The identity of *Paramormyrops sphekodes* and discovery of a new species

Of those species now placed in *Paramormyrops*, the earliest to have been published is *P. sphekodes*, described by H.E. Sauvage (1879) as *Mormyrops sphekodes* from specimens collected at Doumé (0°50.6′S, 12°57.7′E), a village at a cataract in the Ogooué River in what is now the Ogooué-Lolo Province of Gabon, about 28 km upstream of the town of Lastoursville. The collector was Alfred Marche (1844–1898), a naturalist on the first of Pierre Savorgnan de Brazza's exploratory missions for France on the Ogooué River. Marche stayed at Doumé between September 1876 and May 1877 where he collected zoological specimens and anthropological artefacts (Marche, 1879). *M. sphekodes* was one of nine fish species Sauvage described from Marche's Doumé collections, eight of which remain valid.

Without reporting how many specimens he was working from, Sauvage (1879, 1880) indicated that his largest specimen of *M. sphekodes* was 140 mm in total length. He did not designate a holotype specimen. The original MNHN (National Museum of Natural History, Paris) handwritten ledger indicates two specimens of *M. sphekodes* accessioned from Marche's collections under number 893 (personal observation). These two specimens, vertically suspended from a single glass bubble in a tall jar, are seen in Wilhelm Harder's 1984 photograph of A.893 (Harder, 2000) shown in Fig. 1. In 1998, the smaller specimen was removed and catalogued separately as MNHN 1998-1050.

Oddly, Bertin (1940) in his catalogue of MNHN fish types makes no mention of two specimens in MNHN A.893, simply repeating Sauvage's given length of 140 mm for a specimen he calls the 'holotype' (see designation of lectotype in Systematics section).

These two specimens, MNHN A.893 and 1998-1050, are now in rather poor condition and uncertainty regarding correct identification of *P. sphekodes* has been a major impediment to progress in the revision of *Paramormyrops*. In order to improve our ability to correctly identify this species in the field and in museum collections, we sought to make new collections of *P. sphekodes* from the type locality of Doumé. Despite its importance as a type locality for Ogooué fishes, Doumé seems not to have been revisited for scientific

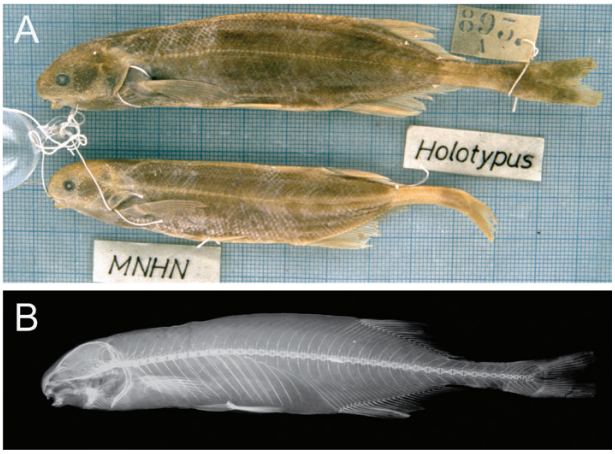

Figure 1. (A) *Paramormyrops sphekodes* (Sauvage, 1877) MNHN A.893 photographed in 1984 by W. Harder at which time the lot contained two specimens, suspended vertically in a tall jar from a glass floater. The original MNHN catalogue shows two specimens accessioned in 1878 under this number. The larger specimen (SL = 113.8 mm) is currently catalogued as A 893; the smaller specimen (SL = 98.7 mm) was subsequently catalogued in 1998 as MNHN 1050-1998. Sauvage's original description indicates multiple specimens with a largest of 140 mm total length, but he designated no holotype. We regard these specimens as syntypes prior to our designation of the larger as lectotype. (B) Radiograph of MNHN A893.

fish collection since 1877. Today Doumé is a small village of a few hundred people and this area of the river – part of a designated Ramsar site ('Rapids of Doumé and Mboungou-Badouma') – remains largely pristine.

J.P. Sullivan made collections of fishes from Doumé and from the Sébé River nearby in 2011 and 2014. From these collections, we identify and redescribe *P. sphekodes* as well as describe a new cryptic species of *Paramormyrops* co-collected with it and at many other sites in the Ogooué River basin. We show how these two species can be distinguished from each other and from other *Paramormyrops* based on EOD waveform, morphology and mitochondrial DNA sequences.

MATERIAL AND METHODS

Fish capture, EOD recording and specimen handling

We collected, handled and euthanized specimens following Guidelines for the Use of Fishes in Research (2004, 2013) from the American Fisheries Society, American Institute of Fishery Research Biologists and American Society of Ichthyologists and Herpetologists.

Cylindrical funnel traps were constructed from XB1132 black polyethylene 0.5 in. diamond mesh (U.S. Netting Inc., Erie, PA, USA), weighted with stones, baited with fresh earthworms and set on river or stream bottom attached to a line and float (Sullivan, 2015). Traps were typically checked every 30 min, and the fish transferred immediately to a large aerated cooler filled with water from the collection site.

We recorded EODs from specimens placed in a small plastic container filled with water from the collection site, using silver/silver chloride electrodes directly connected to the microphone input of an analog-to-digital converter, an Edirol FA-66 (Roland Corporation) or an Echo 2 (Echo Digital Audio, Inc.) sampling at 192 kHz/16 bits, connected to the Firewire or USB input of a laptop computer (Hopkins *et al.*, 2007, Sullivan, 2016). We visualized and saved signals using SignalScope virtual oscilloscope software (Faber Acoustical, LLC). The polarity of each discharge was noted, and recorded and graphed with head-positive voltages upward. The water temperature, noted at the time of recording, varied between 19.3 and 31.0 °C over 622 EOD recordings (average = 25.46 °C ± 2.09 standard deviation). In order to compare EODs recorded at different temperatures, we normalized the time base of all EOD waveforms to a uniform temperature of 25 °C by adjusting the digital sampling rate, R_T, to R_{25} the sampling rate at 25 °C, using the temperature coefficient formula for rate functions

$$R_{25} = R_T \cdot Q_{10}^{(25-T)/10}$$

with a Q_{10} value of 1.6, established empirically from a captive population of *Petrocephalus soudanensis* and *Brienomyrus brachyistius* recorded over 3 weeks with fluctuating temperatures (Hopkins, unpublished data). After recording, the fish were euthanized with an overdose of the anaesthetic MS222 (tricaine methanesulfonate), tagged with permanent specimen numbers, sampled for tissue using clips from right pectoral or pelvic fins, or from right dorsal hypaxial muscle, and then fixed in 10% formalin. Specimens were subsequently transferred to 70% ethanol and deposited in the Cornell University Museum of Vertebrates (CUMV) in Ithaca, New York, with corresponding catalogue numbers.

Morphometrics and meristics

We took 23 point-to-point measurements with a digital calliper following procedures from Boden, Teugels & Hopkins (1997): total length (TL); standard length (SL); caudal peduncle depth (CPD); caudal peduncle length (CPL); head length (HL); head depth (HD); snout length (SNL); interorbital width (IOW); eye diameter (ED); post-orbital length (POL); body depth (BD); pre-dorsal distance (PDD); pre-anal distance (PAD); pre-pelvic

distance (PPLD); pre-pectoral distance (PPCD); dorsal fin length (DFL); dorsal fin height (DFH); anal fin length (AFL); anal fin height (AFH); pelvic fin length (PLFL); pectoral fin length (PCFL); distance between pelvic and anal fins (DPLAF) and distance between pectoral and anal fins (DPCAF). We made the following modifications to two measurements in Boden *et al.* (1997): head width (HW) was measured at the maximum width of the head and mouth width (MW) was measured as the maximum lateral distance between inner corners of the front of the mouth (see Table 1 for abbreviations).

In addition, we made five measurements not described in Boden *et al.* (1997): BD at the urogenital pore (BDUGP), defined as the vertical distance from the urogenital pore opening to the dorsal margin of the body; BD at the pectoral fin (BDPCF), the vertical distance between the ventral to dorsal body margin at the level of the pectoral fin origin; HL to the bony operculum (HLBO), defined as the point-to-point distance from anterior tip of snout (upper jaw) to posterior margin of the opercular bone and two distance measures taken from x-rays: HLx, the HL measured from the anterior tip of the mesethmoid to the posterior face of the first vertebral centrum and HDx, the HD measured from the ventral medial junction of the cleithra and anterior junction supraoccipital and parietal bones of the skull. All distances taken from x-rays lie on the median plane of the specimen and care was taken to orient the medial plane of the specimen parallel to the x-ray film. We determined the angles spanned by the snout and head as follows:

$$\text{Snout angle} = \frac{180}{\pi} \bullet 2 \bullet \arcsin\left(\frac{\text{SNL}+\frac{\text{ED}}{2}}{\frac{\text{IOW}}{2}}\right)$$

$$\text{Head angle} = \frac{180}{\pi} \bullet 2 \bullet \arcsin\left(\frac{\frac{\text{HW}}{2}}{\text{HL}}\right)$$

Ten meristic measurements follow Boden *et al.* (1997): total dorsal-fin rays (DFR); total anal-fin rays (AFR); pectoral-fin rays (PCFR); pelvic-fin rays (PLFR); penetrated scales on the lateral line (SLL); rows of scales from anterior of dorsal fin up to, not including, lateral line (SDL); rows of scales from anterior base of pelvic fin up to, not including, lateral line (SPL); scales around middle of caudal peduncle (SCP); upper-jaw teeth (TUJ) and lower-jaw teeth (TLJ).

For all *Paramormyrops*, the first two dorsal and anal fin rays are unbranched, unsegmented and so small they are difficult to see without a radiograph. These two unbranched and unsegmented rays are followed by a single unbranched, segmented ray (the first long ray), followed by numerous branched, segmented rays. The last dorsal and anal ray is usually branched all the way to its origin, but it is counted as one ray. In

Table 1. Abbreviations of morphometrics and meristics. Details of how measurements are taken are given in Material and Methods section

Morphometrics	
AFH	Anal fin height
AFL	Anal fin length
BD	Body depth at pectoral fin
BDUGP	Body depth urogenital pore
CPD	Caudal peduncle depth
CPL	Caudal peduncle length
DFH	Dorsal fin height
DFL	Dorsal fin length
DPCAF	Distance between pectoral and anal fins
DPLAV	Distance between pelvic and anal fins
ED	Eye diameter
HANG	Head angle
HD	Head depth
HDx	Head depth from x-ray
HL	Head length
HLBO	Head length to opercular bone
HLx	Head length from x-ray
IOW	Interorbital width
PAD	Pre anal distance
PCFL	Pectoral fin length
PDD	Pre dorsal distance
PLD	Pre pelvic distance
PLFL	Pelvic fin length
POL	Post orbital length
PPCD	Pre pectoral distance
SANG	Snout angle
SL	Standard length
SNL	Snout length
TL	Total length
Meristics	
AFR	Anal fin rays
AV	Anterior vertebrae
CV	Caudal vertebrae
DFR	Dorsal fin rays
PCFR	Pectoral fin rays
PCV	Precaudal vertebrae
PLFR	Pelvic fin rays
SCP	Scales around caudal peduncle
SDL	Dorsal scales
SLL	Pierced scales in lateral line
SPL	Ventral scales from pelvic fin
TLJ	Teeth in lower jaw
TUJ	Teeth in upper jaw
TV	Total vertebrae

addition to total ray counts, DFR and AFR, we counted branched dorsal-fin rays (BDFR) and branched anal-fin rays (BAFR).

We made the following counts from x-rays: total vertebrae (TV), the number of vertebrae counted from the base of the skull up to, but not including, the last demicentrum fused to the hypural plate; caudal vertebrae (CV), defined as vertebrae not carrying ribs with complete or present haemal arches up to, but not including, the last demicentrum fused to the hypural plate and pre-caudal vertebrae (PCV), defined as the number of centra starting with the centrum fused to the skull base with a small neural spine, ending with the centrum before the first caudal vertebra. Abbreviations are reiterated in Table 1.

We determined the sex of specimens by examining the base of the anal-fin ray for an anal-fin notch, an indentation in the anal-fin base and the thickening at the base of the anal fin rays of the anterior third of the anal fin both found only in males (Pezzanite & Moller, 1998).

Morphometric ratios were plotted in JMP Pro 12 software (SAS Institute Inc., 2012). We used built-in JMP functions to compute descriptive statistics, parametric, non-parametric and multi-variate statistics.

DNA SEQUENCING AND PHYLOGENETIC ANALYSIS

Complete mitochondrial cytochrome *b* (cyt-*b*) genes (1140 bp) were amplified by PCR and sequenced for eight specimens that we recognized as an undescribed *Paramormyrops* sp. 'SN4' (see Sullivan *et al.*, 2002) from its morphology and its EOD (two from the Sébé site, six from Doumé) and nine of the short-EOD forms (six from the Sébé site and three from Doumé) using DNA extracted from fin clips or epaxial muscle tissue preserved in 95% ethanol. From a subset of these (four specimens of each type) we additionally sequenced the 'barcode' segment of the cytochrome oxidase I gene (COI). We used the following PCR primers for amplification and sequencing for cyt-*b* (L14724) GAC TTG AAA AAC CAC CGT TG, (H15915) CTC CGA TCT CCG GAT TAC AAG AC; for COI, (COIF-Peng) TCT CAA CCA ACC ATA AAG ACA TTG G & (COIR-Peng) TAT ACT TCT GGG TGC CCA AAG AAT CA. We compared the cyt-*b* sequences to those determined previously (Sullivan *et al.*, 2002, 2004), including ten undescribed species we have given provisional code names as follows: SN2, SN3, SN4, SN7, BN2, BP5, BP6, OFF, PAR and NGO. The codes refer to species that have sharp or blunt snouts (S or B, respectively), non-penetrating electrocytes or penetrating electrocytes (N or P, respectively), followed by a number. The last three codes are shortened manuscript names for three species with sharp snouts.

We carried out PCR in 20 µL reactions with components at the following concentrations: 1× Sigma PCR buffer (Sigma–Aldrich, St. Louis, MO), 0.02 U/µL Sigma JumpStart *Taq*, 2 mM $MgCl_2$, 0.4 µM of forward and reverse primer, 200 µM of each dNTP and approximately 200 pg/µL template DNA. We used an initial denaturation step of 1 min at 94 °C followed by 30 or 35 cycles of 94 °C for 30 s, annealing at temperatures between 48 and 57 °C for 30 s, and extension at 72 °C for 1.5 min. Finally, we set a 10 min, 72 °C extension step. Amplification success was evaluated on ethidium bromide-stained agarose gels. We purified PCR products using ExonucleaseI and Shrimp Alkaline Phosphatase and performed dye-deoxy termination cycle sequencing using ABI Big Dye chemistry (PE Applied Biosystems, Foster City, CA). Sequencing reactions were cleaned on Sephadex columns prior to sequencing on an ABI capillary sequencer.

We edited and combined sequences into contigs for each fragment with Sequencher 4.2 (GeneCodes Corporation, Ann Arbor, MI) or CodonCodes Aligner (CodonCode Corporation, Centerville, MA).

We added these sequences to the alignment published in Sullivan *et al.* (2004) that includes 73 other *Paramormyrops* cyt-*b* sequences. Alignment was unambiguous. Using *M. ntemensis* as outgroup, we performed a maximum likelihood phylogenetic analysis of this matrix in RAxML v.8, implemented on XSEDE (Stamatakis, 2014) via the CIPRES Science Gateway web server (Miller, Pfeiffer & Schwartz, 2010) using separate GTR + G evolutionary models for each codon position and performed a non-parametric bootstrap analysis to estimate support for nodes. All other settings were left at their default values.

RESULTS

TWO MODAL EOD TYPES AMONG THE *PARAMORMYROPS* FROM DOUMÉ

We identified 40 specimens of *Paramormyrops* from the Ogooué River at Doumé and from the nearby Sébé River that closely resemble the two specimens that were used to describe *P. sphekodes* (Sauvage, 1879). These 40 specimens had tooth, scale and ray counts and sharp snouts matching the lectotype of *P. sphekodes* to the exclusion of all other described *Paramormyrops*. However, EOD waveforms from each of these 40 specimens revealed two modal EOD types differing in the overall pulse duration (Fig. 2A–C). Four specimens from the Chutes de Doumé and five from the Sébé River had shorter EODs averaging 0.815 ± 0.352 ms (mean ± SD) duration, while 20 specimens from Doumé and 11 from the Sébé River had longer EODs averaging 4.4 ± 1.24 ms. The longer EOD

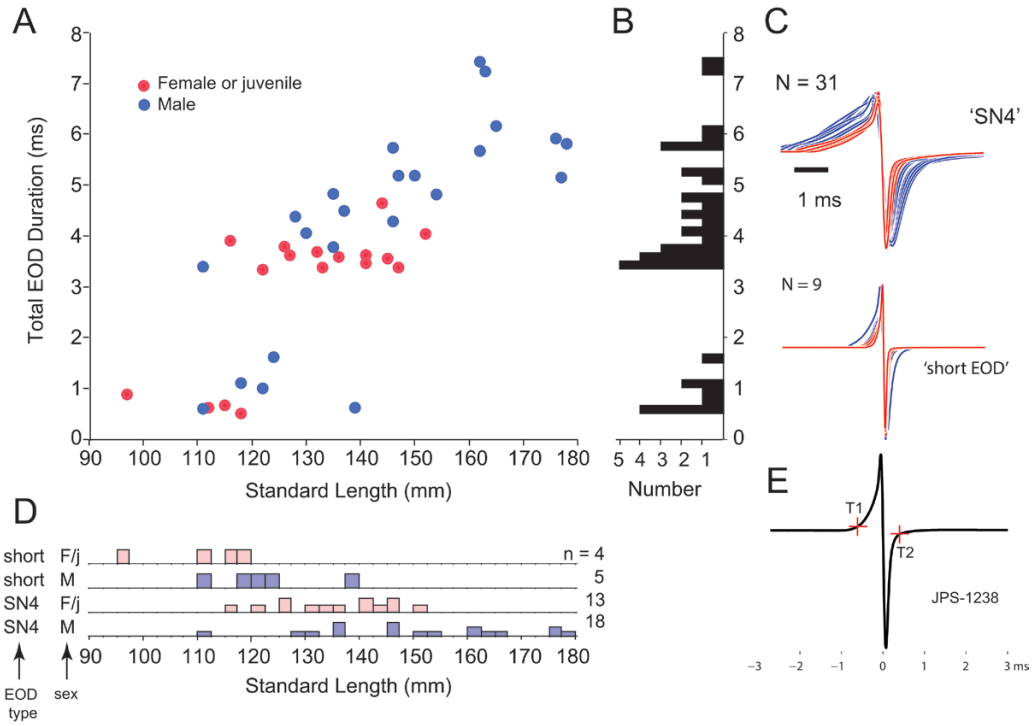

Figure 2. Electric organ discharge (EOD) waveforms recorded from 40 specimens of *P. sphekodes*-like mormyrids from the Ogooué River Basin of Gabon suggest the possibility of two species with distinct EOD waveforms. (A) For each specimen, EOD duration is plotted against standard length (SL). (B) Histogram of EOD durations reveals two modal peaks: one for short EODs, < 2 ms duration, and one for longer EODs, > 2 ms. (C) EOD waveforms of longer (above) and shorter duration (below) are superimposed after each EOD's amplitude is normalized to the same peak-to-peak height and centred on the zero-crossing between positive and negative peaks. Blue lines are males and red lines are females. Head positivity is upward. EOD duration is measured between T1 and T2 (in E), first and last points of the waveform that deviate above or below the baseline by more than 2% of the peak-to-peak height. In previous publications, the longer EOD type was referred to by the code name 'SN4'. The fish with the 'short EOD' waveform is new to this study. (D) Histograms of SLs of all 40 specimens separated by EOD-type and by sex/age class show that within each EOD type there are males recognized by their dimorphic anal fins. Within each group, males tend to have the longest duration waveforms. This sex difference is especially pronounced for SN4 males recorded during the breeding season. Fish of both EOD types co-occur at two sites in Gabon: the main channel of the Ogooué River at Doumé and the Sébé River nearby (see map). (E) EOD waveform of specimen CUMV 98177 tag JPS-1238 showing how EOD duration is measured.

specimens had discharges, size and body morphology that we had recognized from earlier collections and we had referred to it using the code name of SN4 (Sullivan *et al.*, 2002, 2004), but the shorter duration EOD was new to us. We had not previously recorded such a short waveform from a *Paramormyrops* from the lower, middle, or upper Ogooué or any of its tributaries. Because of the bimodal distribution of EOD durations, we had reason to suspect that the 40 specimens from Doumé, although resembling *P. sphekodes*, actually represent more than a single species.

Meristics

Although tooth, scale and ray counts are helpful in diagnosing some species of *Paramormyrops*, we could not distinguish these two signal types on the basis of meristics. We compared DFR, AFR, SLL, SDL, SPL, TUJ, TLJ, AV and CV from the specimens of the two EOD types using principal component analysis. Although the first principal component scores are slightly more positive for the short EOD specimens compared to the SN4 specimens, the difference is not statistically significant and the scores are widely overlapping. PC1 is most heavily weighted by the total number of lateral line scales and the total number of vertebrae but the short EOD form and SN4 cannot be distinguished using either character. PC2 is most strongly weighted by SPL and AFR but neither of these measures differed between groups. We conclude that meristics cannot be used to distinguish the fish of these two signal forms. By contrast, the undescribed species given the

code name *P.* sp. *'OFF'* collected with these other specimens could be distinguished from either of these two types by having 16 caudal peduncle scales instead of 12 and by the appearance of the head (Fig. 16).

Morphometrics

Short EOD individuals are smaller than SN4 individuals on average (Fig. 2D) even though both types were collected together in the same fish traps, from each of the two most recent collection localities. To explore the possibility that EOD duration might change during development, as is the case for some mormyrids in the genus *Campylomormyrus* (Feulner *et al.*, 2006, 2007, 2008), we looked for sexually dimorphic traits in the anal fin (Material and Methods) in all specimens of both signal types. We used dimorphic traits as an early indicator of adult body size. Specimens lacking proximal thickening of the base of anal rays with no measurable indentations along the base of the anal fin were classified as juvenile or female (Greisman & Moller, 2005). Figure 2D shows histograms of SLs of short EOD specimens and SN4 specimens separated by sex/age class and signal type. Since both EOD groups include females/juveniles as well as dimorphic males, it is unlikely that the large difference in EOD duration between these two groups can be attributed to age, gender, or sexual maturity. Sex differences in EODs of each sub-group are illustrated in Fig. 2C and discussed further in the following.

We next compared morphometric ratios of the short EOD group and the SN4 group and found three measures that differ between the two (Figs 3, 4). They are as follows: (1) snout angle or the ratio IOW/SNL which is highly correlated with snout angle (Fig. 5D); (2) CPD/CPL and (3) HLx/HDx, the ratio of HL to HD taken from x-rays. Other morphometric ratios that differed between signal groups with overlap included ED/HL and BD/BDUGP, both of which are higher in the short EOD form compared to the SN4 form. These morphometric ratios are summarized in the descriptive systematic section and illustrated in Fig. 5. The short EOD specimens had increased snout angles and IOW/SNL ratios, as well as reduced CPD/CPL and reduced HLx/HDx compared to the SN4 (Figs 3, 4). Additional morphometric ratios (Fig. 5, Table 2) help to distinguish short EOD fish from SN4 fish and either of these from *Paramormyrops curvifrons*, another similar *Paramormyrops* known from the Ivindo River of Gabon. The most reliable characters for morphometric diagnosis of these three are snout angle (or IOW/SNL) and HLx/HDx which requires use of radiographs.

The clear differences in morphometric characters between fish with different signal types lend support to the hypothesis that these represent two separate species.

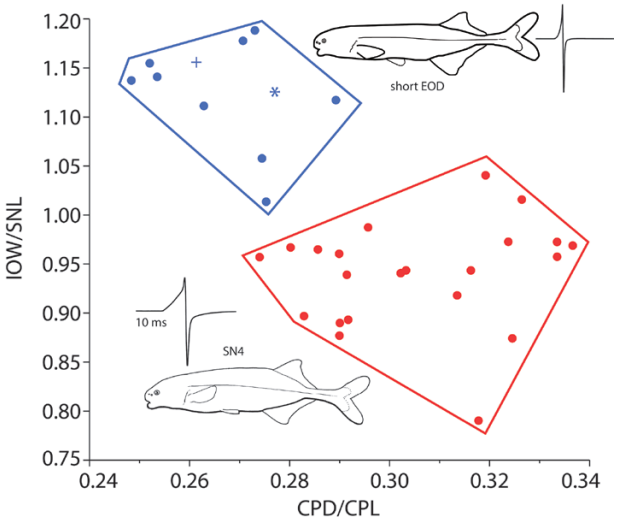

Figure 3. The *Paramormyrops* specimens with short EODs, and those called SN4 have overlapping meristics but differ in a number of morphometric ratios. Here, the short EOD specimens are shown as blue circles, while '∗' indicates the lectotype of *P. sphekodes* and '+' indicates the paralectotype. The red circles show those with longer EODs referred to as SN4 specimens. The short EOD forms have elevated ratios of interorbital width to snout length and correspondingly blunter snout angles than the SN4 specimens. They also have slightly reduced caudal peduncle depth to length ratios. There is overlap in each ratio taken separately, but combined they provide a convenient morphological basis for diagnosis between these two EOD types. EOD traces are 10 ms long.

Comparison with existing types

We compared the morphometric ratios of the 40 specimens representing the two EOD groups to the two preserved specimens in the National Museum of Natural History, Paris (MNHN), including the type of *P. sphekodes* (Fig. 1A, B). Figures 3 and 4 show that both MNHN A.893 and MNHN 1989-1050 fall within the range typical of the short EOD form. Although the two ratios plotted in Fig. 3, IOW/SNL and CPD/CPL, cannot by themselves diagnose the two EOD types, in combination they provide good separation. The ratio of HL to HD (HLx/HDx) measured from radiographs using well-defined osteological landmarks (Fig. 4) shows no overlap between EOD types. A similar measure, HL/HD, taken with digital callipers is too variable to distinguish the two species owing to lack of fixed bony landmarks for HD measurements (Fig. 5C). The HDx and HLx measurements correct this problem and enable reliable diagnosis. From these morphological results we conclude that the short EOD form matches the type material of *P. sphekodes* collected by Marche and described by Sauvage, while the SN4 form

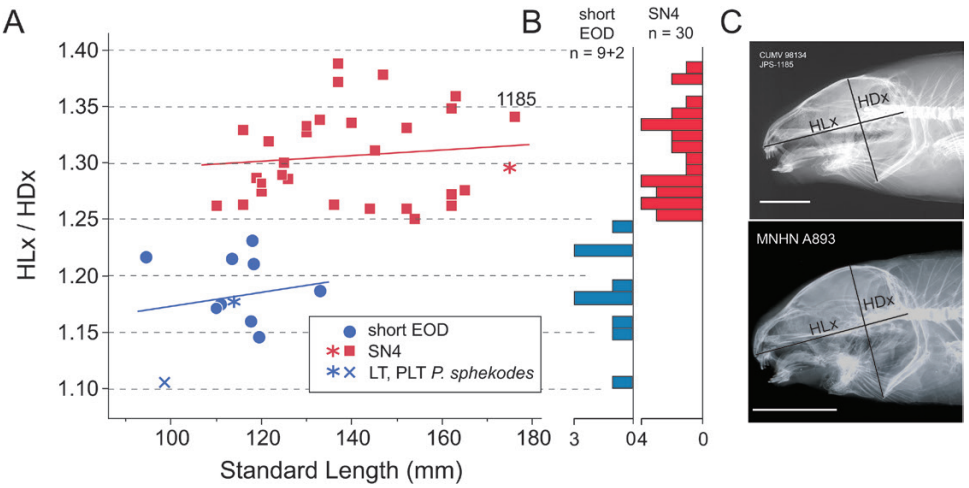

Figure 4. The short EOD and SN4 *Paramormyrops* differ in the ratio of head length (HL) to head depth (HD) when measurements are taken from radiographs. (A) HLx/HDx is plotted against standard length for 41 specimens including short EOD specimens (n = 9, blue circles), SN4 specimens (n = 30, red squares) and the two existing types (* = lectotype of *P. sphekodes* and 'x' = the paralectotype). Solid lines show linear regression lines showing that head shape changes little with overall size. The measurements of the lectotype (LT) of *P. sphekodes* (MNHN-A893) and paralectotype (PLT) (MNHN 1998-1050) identify the short EOD individuals as *P. sphekodes*. The specimens with SN4-type EODs belong to a new species (red * indicates the new species holotype). Specimen 1185 is shown in x-ray in C. (B) Non-overlapping histograms of HLx/HDx allow for good diagnosis of the two EOD types even if no EOD is available, as with the two types of *P. sphekodes*. (C) Radiographs of two specimens (Specimen CUMV 98134 tag number JPS-1185, an SN4 fish and MNHN-A893) illustrate landmarks used for measuring HLx and HDx (see Material and Methods). Scale bars = 1 cm.

represents a new species which we describe in the following section.

Phylogenetics

GenBank numbers for the cyt-*b* sequences produced for this study are given in Table 4. The portion of ML tree produced by the analysis in RAxML on which cyt-*b* haplotypes from the SN4 and short EOD individuals appear is shown as a phylogram in Fig. 6.

Most of the short EOD *Paramormyrops* cluster in an exclusive clade with one specimen grouped with undescribed species coded as 'NGO' (Fig. 6) while *Paramormyrops* SN4 clusters with *P. curvifrons* and *P. longicaudatus*, with one haplotype appearing in another clade with two undescribed species coded as 'SN7' and 'SN2'. In no case do we see specimens with short EODs and fish with SN4 EODs sharing cyt-*b* haplotypes, or appearing as closest relatives. Repeated mitochondrial introgression is often seen across species boundaries within *Paramormyrops* and few species within the genus are monophyletic with respect to mitochondrial DNA sequences (Sullivan *et al.*, 2002, 2004). However, the observation of phylogenetic separation between mitochondrial haplotypes of short EOD and SN4 individuals collected together is strong evidence for heterospecificity of the two EOD forms.

SYSTEMATICS

Designation of a lectotype for *M. sphekodes* Sauvage, 1879

The *Catalog of Fishes* (Eschmeyer, 2015) and Gosse (1984) follow Bertin (1940) in indicating that there is a holotype by monotypy for *M. sphekodes*, but this is an error. As noted above, Sauvage (1879, 1880) indicated more than one specimen but never designated a holotype. All evidence including the hand-written accession log at the MNHN suggests that MNHN A.893 contained two specimens collected by Marche at Doumé until 1998 when the smaller specimen was catalogued separately as 1998-1050 (Fig. 1).

Given these facts, the two original specimens accessioned under A.893 must be regarded as syntypes ICZN (1999):72.1.1. In our view, Bertin's catalogue entry does not fulfil the requirements of ICZN (1999):74.6 for fixation of a lectotype and so this is left for us to do here. For the sake of stability, it makes sense to designate the larger of the two specimens as lectotype, the one currently regarded – in error – as the holotype of *M. sphekodes*. This specimen has suffered damage to the end of the caudal fin, making comparison to Sauvage's length measurement difficult. Adding 16% to its SL (the mean difference between SL and TL in fresh *Paramormyrops* specimens) gives us an estimate of 132 mm for TL, short of Sauvage's

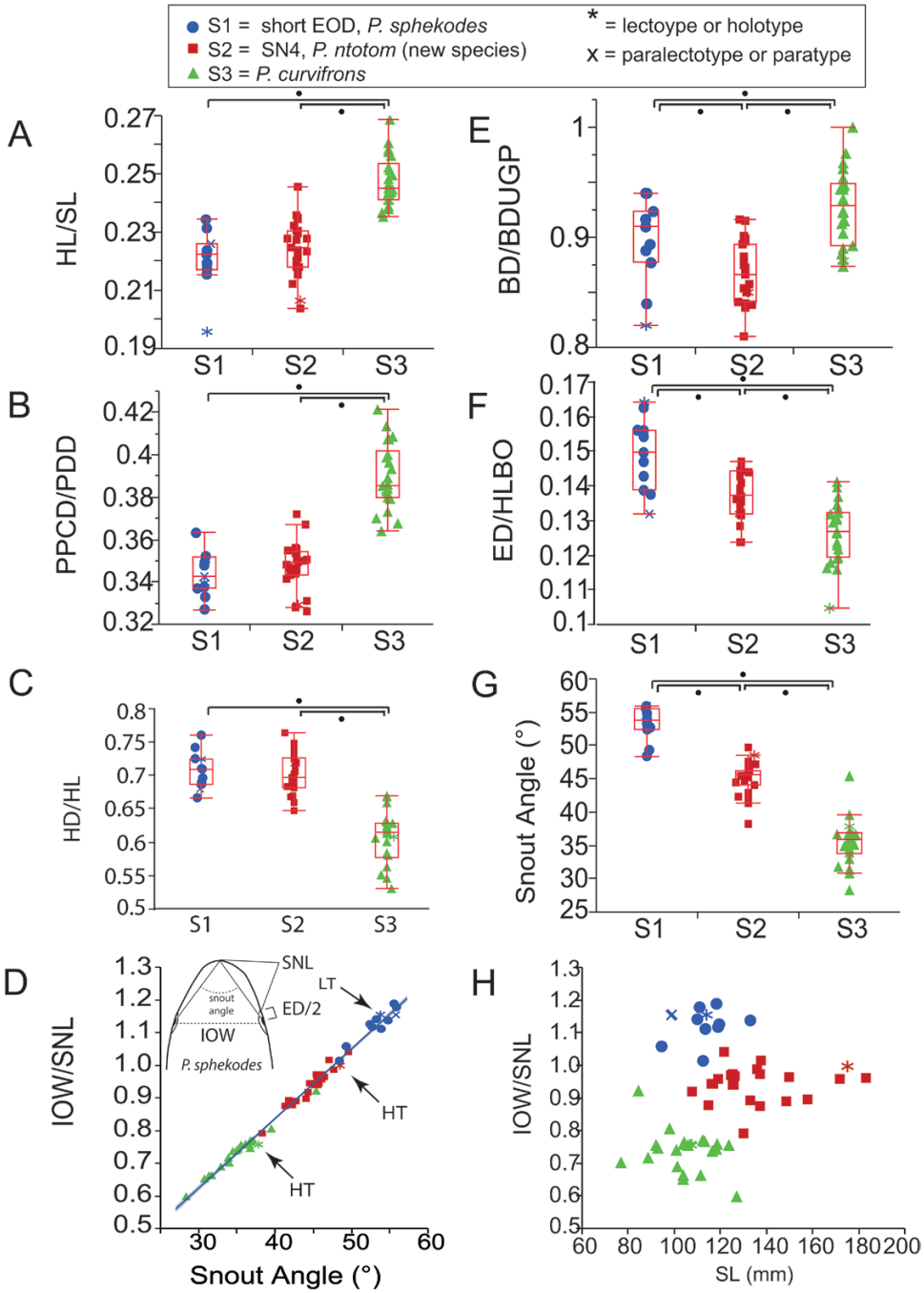

Figure 5. Morphometrics and ratios from the three species of *Paramormyrops* included in this study. (A–C) and (E–G) show measurement ratios useful in diagnosis of these three species. Snout angle measurements (see Material and Methods) are compared in (D) and (G). (D) plots snout angle against IOW/SNL. Holotypes or lectotypes are indicated by '*' symbols and paratypes are indicated by 'x' symbols. (H) compares IOW/SNL for specimens of differing standard lengths. Superimposed on the data points in (A–C) and (E–G) are box plots showing range, 25% quartile, median and 75% quartile. Black bars above box plots span samples where means differ significantly ($P \leq 0.05$) using Tukey–Kramer multiple comparison tests for differences in sample means. See Table 1 for abbreviations.

140 mm. However, we routinely see length shrinkage of 6–8% of *Paramormyrops* specimens in alcohol. We hereby designate the single specimen now catalogued under MNHN A.893, measuring 113.9 mm SL, lectotype of *M. sphekodes* Sauvage. MNHN 1998-1050, originally the second specimen catalogued as A.893

Table 2. Morphometrics and meristics from 53 specimens of *Paramormyrops*

	P. sphekodes				***P. ntotom* sp. nov.**				***P. curvifrons***			
	Lectotype (mm)	Others (**average**)	(n = 10) (SD)		Holotype (mm)	Paratypes (average)	(n = 22) (SD)		Holotype (mm)	Others (average)	(n = 21) (SD)	
Morphometrics												
TL (Total length)	126.4	128.7	12.9		201.0	150.7	19.9		121.8	118.4	14.6	
SL (Standard length)	113.9	113.0	10.9		175.0	133.9	18.7		107.3	104.7	13.0	
HL (Head length)	22.3	25.2	2.1		36.1	30.1	3.2		25.8	25.9	3.0	
Percent of SL		**Minimum**	**Median**	**Maximum**		**Minimum**	**Median**	**Maximum**		**Minimum**	**Median**	**Maximum**
BD (Body depth)	16.8	15.4	16.1	17.3	15.6	14.9	16.3	18.1	17.3	13.5	15.9	19.5
BDUGP (BD at urogenital pore)	20.5	17.1	17.6	19.5	18.3	16.7	18.7	21.5	19.7	14.8	16.8	20.3
CPL (Caudal peduncle length)	19.4	17.3	18.6	20.0	16.8	15.8	17.6	19.3	21.6	16.4	20.3	22.9
HL (Head length)	19.6	21.5	22.2	23.4	20.6	20.4	22.6	24.6	24.1	23.5	24.5	26.9
PPCD (Pre pectoral dist.)	22.0	21.2	22.2	23.3	20.6	20.4	22.1	23.5	24.3	22.8	24.7	27.5
PPLD (Pre pelvic dist.)	38.8	35.0	37.3	38.8	35.5	34.6	36.9	38.6	39.1	36.3	38.0	39.6
PDD (Pre dorsal dist.)	64.7	63.8	64.1	65.2	62.6	61.3	63.5	66.1	63.4	61.8	63.2	65.5
PAD (Pre anal dist.)	59.9	55.9	57.7	61.0	57.1	55.9	57.7	59.8	58.9	56.0	57.5	58.7
PCFL (Pre pectoral dist.)	16.5	12.4	16.0	17.0	14.8	14.6	15.8	16.8	16.2	14.4	15.9	17.8
PLFL (Pelvic fin length)	11.0	9.2	10.1	10.8	9.7	8.2	10.0	10.8	10.4	9.1	10.2	12.0
DFL (Dorsal fin length)	19.1	17.3	19.0	20.7	21.3	17.2	19.2	20.7	19.1	18.8	19.9	21.8
AFL (Anal fin length)	20.7	21.9	23.2	24.5	25.7	21.4	22.9	24.9	23.9	21.9	23.9	25.5
Percent of HL												
HD (Head depth)	72.4	66.7	70.3	76.0	71.9	64.8	69.6	79.8	60.7	53.1	61.6	67.0
SNL (Snout length)	27.2	23.8	24.9	26.5	26.9	23.8	26.3	28.3	27.3	23.3	25.9	29.1
IOW (Inter orbital width)	31.4	26.8	28.0	29.3	26.8	22.4	24.4	27.4	20.7	15.2	19.1	25.5
ED (Eye diam.)	15.0	11.2	12.7	13.7	11.5	10.6	12.0	13.3	9.1	10.2	11.3	12.4
ED%HLBO (Head length at operc. bone)	16.4	13.2	14.8	16.3	13.2	12.4	13.8	14.7	10.5	11.6	12.7	14.1
POL (Post orbital length)	62.8	60.8	64.7	68.4	66.2	64.0	65.9	68.1	64.5	62.7	68.0	72.2
Other												
DFH%DFL (Dorsal fin height % DF length)	83.2	62.3	70.6	79.2	60.1	59.0	68.1	77.8	71.7	60.9	72.3	78.8
AFH%AFL (Anal fin height % AF length)	71.8	45.2	62.2	65.0	41.3	50.4	58.5	65.9	67.6	56.8	66.2	72.2
DFL%AFL	92.2	74.1	83.4	86.8	82.9	78.4	82.9	88.4	80.0	76.5	83.1	95.0
PPCD%PDD	33.9	32.7	34.5	36.3	32.9	32.6	35.0	37.2	38.3	36.4	38.6	42.2
BD%BDUGP	82.0	84.0	91.0	94.0	85.0	81.1	86.6	91.6	87.9	87.4	93.4	99.9
CPD%CPL (Caudal peduncle depth%CPL)	26.1	24.8	27.2	28.9	29.7	27.4	30.3	33.7	18.9	20.1	22.9	27.9
HANG (Head angle)	26.5	22.2	23.9	26.1	25.9	22.1	24.6	27.1	26.7	22.0	24.6	29.0
SANG (Snout angle)	53.8	48.4	53.6	55.9	48.5	38.3	45.5	49.6	37.8	28.4	35.5	45.4

	P. sphekodes				***P. ntotom* sp. nov.**				***P. curvifrons***			
	Lectotype	Others (Minimum)	(n = 10) (Median)	Maximum	Holotype	Paratypes (Minimum)	(n = 22) (Median)	Maximum	Holotype	Others (Minimum)	(n = 21) (Median)	Maximum
Meristics												
DFR (Dorsal fin rays)	21	20	21	23	21	19	20	21	20	20	21	22
AFR (Anal fin rays)	25	24	26	28	26	24	25	26	25	24	25	27

Table 2. Continued

Meristics	*P. sphekodes*				*P. ntotom* sp. nov.				*P. curvifrons*			
	Lectotype	Others (Minimum)	(n = 10) (Median)	Maximum	Holotype	Paratypes (Minimum)	(n = 22) (Median)	Maximum	Holotype	Others (Minimum)	(n = 21) (Median)	Maximum
PCFR (Pectoral fin rays)	10	11	11	11	11	10	11	12	11	9	11	12
PLFR (Pelvic fin rays)	6	6	6	6	6	6	6	6	6	6	6	7
TV (Total vertebrae)	44	43	44	45	44	41	43	44	44	43	44	45
AV (Anterior vertebrae)	18	18	18	19	19	18	18	18	19	18	19	19
CV (Caudal vertebrae)	26	24	24	26	25	22	24	25	25	24	25	26
SLL (Pierced scales in lateral line)	72*	63	67	68	68	57	64	68	62	61	65	69
SDL (Dorsal scale rows)	10	9	11	11	10	9	11	12	10	9	11	12
SPL (Ventral scale rows from pelvic fin)	11	10	13	15	13	10	13	14	9	10	12	14
SCP (Scales around caudal peduncle)	12	12	12	12	12	12	12	12	12	12	12	12
TUJ (Teeth upper jaw)	5	4	5	5	4	4	5	5	5	5	5	5
TLJ (Teeth lower jaw)	6	5	6	6	6	3	6	7	6	6	6	6

*Count unreliable because of damage to specimen.

(109.0 mm TL and 98.7 mm SL), therefore becomes a paralectotype.

PARAMORMYROPS TAVERNE, THYS VAN DEN AUDENAERDE, & HEYMER 1977

Paramormyrops Taverne *et al.*, 1977: 634, type species: *Paramormyrops gabonensis* Taverne, Thys van den Audenaerde, & Heymer 1977.
Mormyrus Linnaeus, 1758 *s.l.* (*partim*)
Mormyrops Müller, 1843 *s.l.* (*partim*)
Marcusenius Gill, 1862 *s.l.* (*partim*)
Hippopotamyrus Pappenheim, 1906 *s.l.* (*partim*)
Brienomyrus Taverne, 1971 *s.l.* (*partim*)
Pollimyrus Taverne, 1971 (*partim*)

Revised diagnosis: Body moderately elongate, not deep, moderately compressed laterally. Dorsal and ventral profiles nearly parallel from occiput to level of anal fin origin. BD 15–25% of SL. HL approximately equal to or slightly greater than the BD, snout non-tubular. Frontal profile slightly concave or convex and rounded; head and snout profile blunt and rounded (U-shaped) or sharp and tapering (V-shaped) when viewed dorsally. Mouth small and terminal to sub terminal; teeth bicuspid and pincer-like, 5–7 in upper jaw, 6–8 in lower. Chin fleshy, usually somewhat bulbous, covered with electroreceptors, not forward-protruding. Dorsal and anal fins originating well posterior to mid-body length; anal fin equal to or slightly longer than dorsal and containing a few additional rays. Base of last anal and last DFR vertically aligned. Distal tips of last AFR and DFR also vertically aligned. Nostrils well separated and positioned approximately halfway between eye and tip of snout. Electrocytes, type Pa (*P*enetrating stalks with *a*nterior innervation) or NPp (*N*on-*P*enetrating stalks with *p*osterior innervation). Mesethmoid curved, lateral ethmoid reduced or absent. DFR 15–23 total simple, unbranched and branched. AFR 21–29 total. Origin of pelvic fins closer to pectoral than to anal. Total lateral line scales 53–78; circumpeduncular scales 12–20; total vertebrae 40–47. Urophore complex with ventral hypurals 1 and 2 usually unfused in adults often fused in juveniles.

Comparisons: Paramormyrops lacks the large chin swelling or chin barbel of *Gnathonemus, Campylomormyrus*, *Genyomyrus* and *Marcusenius*. In adult *Paramormyrops*, BD (15–25% SL) is shallower (i.e. body more elongate) than *Pollimyrus*, *Petrocephalus*, *Stomatorhinus*, *Brevimyrus*, *Boulengeromyrus*, *Ivindomyrus*, *Cryptomyrus* and most *Marcusenius***.** In *Paramormyrops* nostrils are well separated, with the posterior nostril closer to anterior nostril than to eye, unlike *Pollimyrus* and *Ivindomyrus*, and remote from the mouth, unlike

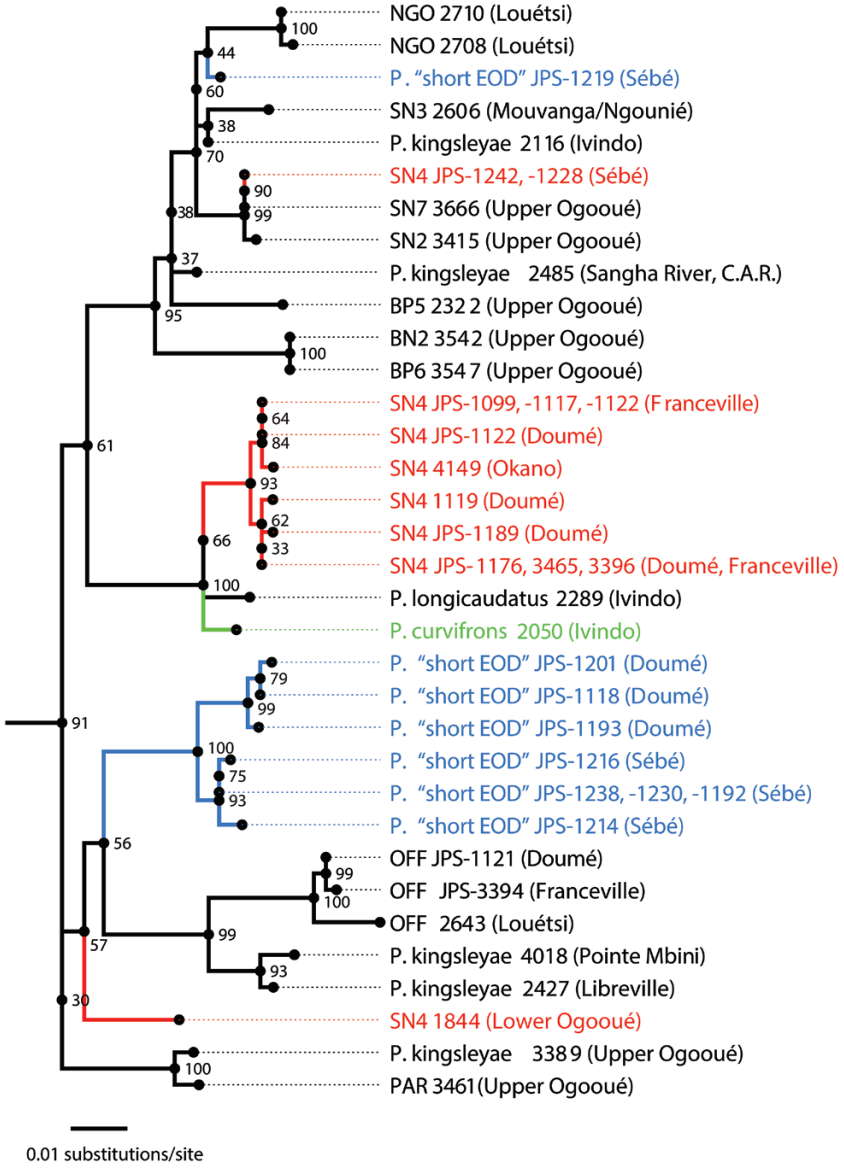

Figure 6. Relevant portion of the phylogram produced from maximum likelihood analysis in RAxML of cyt-*b* sequences from nine individuals of the 'short EOD' form (blue), eight specimens of species 'SN4' from the Doumé and Sébé sites (red) aligned to data matrix (73 *Paramormyrops* individuals) of Sullivan *et al.* (2002), rooted with sequence of *M. ntemensis* (not shown). Sequence of *P. curvifrons* individual is shown in green. For species codes, follow Sullivan *et al.* (2002). Bootstrap values are shown at nodes (filled circles). Haplotypes of SN4 and 'short EOD' do not constitute monophyletic groups. However, no haplotypes are shared between these forms and nowhere on the tree do haplotypes from the two forms appear as nearest relatives. This result is consistent with the hypothesis of heterospecificity of the two forms.

Stomatorhinus. *Paramormyrops* has more longitudinal scales (53–78) than *Cryptomyrus* (44–45) and dorsal and ventral profiles run parallel over much of the body length between head and dorsal fins compared to the more fusiform body shape in *Cryptomyrus*. In *Paramormyrops*, dorsal and anal fins are similar in length with anal slightly longer, unlike *Mormyrus* and *Isichthys* in which dorsal is much longer or *Hyperopisus* in which anal is much longer. In *Paramormyrops*, anal and dorsal fins terminate at about same level and distal tips of last anal and dorsal rays not offset, unlike *Brienomyrus* in which dorsal terminates in advance of anal and distal tips of last anal ray extend farther posteriorly than those of last dorsal ray. *Paramormyrops* typically lacks a pigmented band between anterior of dorsal and anal-fin bases present in different degrees in *Hippopotamyrus*, *Marcusenius*, *Gnathonemus*, *Campylomormyrus*, *Boulengeromyrus*, *Ivindomyrus*

and *Cryptomyrus*. In *Paramormyrops*, teeth are pincer-like and fewer in number than the 10–36 flattened or bicuspid teeth in each jaw of *Mormyrops* species (see Hopkins *et al.*, 2007).

Etymological note: The genus was named by Taverne *et al.* (1977) not for any taxonomic affinity to the genus *Mormyrops*, but because of the similarly in its elongated body form. Taverne *et al.* (1977) documented marked differences in skeletal morphology between *Paramormyrops* and *Mormyrops*.

PARAMORMYROPS BATESII (BOULENGER, 1906)

Marcusenius batesii Boulenger, 1906: 36. Syntypes: BMNH 1906.5.26:159–160. Type locality: Kribi River at Efulen, Cameroon. [Note: Collector George L. Bates probably collected these specimens while at the American Protestant Mission at Efulen (2.7666667°N, 10.7166667°E) located near a small tributary of the Kribi River (now Kienke River)].

Paramormyrops batesii – Hopkins *et al.*, 2007*: 298*.

PARAMORMYROPS CURVIFRONS (TAVERNE, THYS VAN DEN AUDENAERDE, HEYMER & GÉRY, 1977)

Brienomyrus curvifrons Taverne, Thys van den Audenaerde, Heymer & Géry, 1977: 205, Fig. 2. Holotype: MRAC 75.24-P-132. Type locality: Ivindo River near M'Passa, Makokou, Gabon.

Paramormyrops curvifrons – Hopkins *et al.*, 2007*: 304*.

PARAMORMYROPS GABONENSIS TAVERNE, THYS VAN DEN AUDENAERDE, & HEYMER 1977

Paramormyrops gabonensis Taverne, Thys van de Audenaerde, & Heymer, 1977: 635, Fig. 1. Type species. Holotype MRAC 75-24-P-6 from Ivindo River near M'Passa, Makokou, Gabon.

PARAMORMYROPS HOPKINSI (TAVERNE & THYS VAN DEN AUDENAERDE, 1985)

Brienomyrus hopkinsi Taverne & Thys van den Audenaerde, 1985: 49, Fig. 1. Holotype: MRAC 84-34-P-10. Type locality: Ivindo River near Makokou, Gabon.

Paramormyrops hopkinsi – Hopkins *et al.*, 2007: 294.

PARAMORMYROPS JACKSONI (POLL, 1967)

Marcusenius jacksoni Poll, 1967: 55, Fig. 14. Holotype: Dundo Museum 5575 (unique). Type locality: Nharicumbi village, 12°S, 21°10′E, Longa River tributary of Luena River (Zambesi River basin), Angola.

Paramormyrops jacksoni – Taverne *et al.*, 1977: 640.

Note: Because *Paramormyrops jacksoni* is known from a single specimen from a tributary of the upper Zambezi River in Angola, well outside Lower Guinea and Congo River basins where all other *Paramormyrops* are found, it is likely that this species was incorrectly reassigned to *Paramormyrops* by Taverne *et al.* (1977). Instead it more probably belongs in *Pollimyrus*. This opinion is shared by D. Tweddle and P.H. Skelton (pers. comm.) who have examined specimens of *Pollimyrus* from the Kataba tributary of the Upper Zambezi in neighboring Zambia that are a close match to *P. jacksoni* in meristics, body form, and coloration. Further studies are needed before making a generic reassignment of *P. jacksoni*.

PARAMORMYROPS KINGSLEYAE (GÜNTHER, 1896)

Marcusenius kingsleyae Günther, 1896: 281, Pl.15, Fig. a. Holotype (unique): BMNH 1897.5.5:100. Type locality: Old Calabar, Nigeria. (Note: Type locality is questionable and probably the specimen came from the Ogooué River Basin of Gabon (see Teugels & Hopkins 1998: 200 for remarks on possible error in type locality)].

*Marcusenius cabra*e Boulenger, 1900: 130, Pl.48, Fig. 1. Syntypes MRAC 274–275(2), BMNH 1899.11.27:91 (1). Type locality: Marais de Kop-Malafu, Mayumbe, Congo-Brazzaville (Kouilou-Niari Basin), 5.20°S, 12.3°E. Placed in synonymy by Boulenger (1912): 6.

Paramormyrops kingsleyae – Hopkins *et al.*, 2007: 302.

Note: Pending confirmation from DNA study, we suspect *Pollimyrus kingsleyae eburneensis* Bigorne, 1990, from the Agnébi, San Pedro and Banco Rivers in Ivory Coast, is most probably a species of *Pollimyrus* Taverne, 1971 (not a *Paramormyrops*) and recognize it here as *Pollimyrus eburneensis* (Bigorne, 1990).

PARAMORMYROPS LONGICAUDATUS (TAVERNE, THYS VAN DEN AUDENAERDE, HEYMER & GÉRY, 1977)

Brienomyrus longicaudatus Taverne, Thys van den Audenaerde, Heymer & Géry, 1977: 200, Fig. 1. Holotype: MRAC 75-24-P-290. Type locality: Ivindo River near M'Passa, Makokou, Gabon.

Paramormyrops longicaudatus – Hopkins *et al.*, 2007: 296.

PARAMORMYROPS RETRODORSALIS (NICHOLS & GRISCOM, 1917)

Marcusenius retrodorsalis Nichols & Griscom, 1917: 668, Fig. 2. Holotype (unique): AMNH 6933. Type locality: small forest brook tributary to the Bima River, Niapu, Congo. Uele-Ubangi basin. (Note: Specimen closely resembles *P. kingsleyae* and may represent a Congo basin population of this species.)

PARAMORMYROPS TAVERNEI (POLL, 1972)

Brienomyrus tavernei Poll, 1972: 166, Fig. 2. Holotype: MRAC 79-1-P-137 (ex. Coll. Parc Nat. Upemba). Type locality: Masombwe, Kipepe River, tributary of Tumbwe River, Upper Lulalaba (Congo) basin, Democratic Republic of Congo. (Note: Because the type locality of this species is far removed from all other *Paramormyrops*, our reassignment is tentative pending additional molecular, morphological and electrophysiological studies.)

PARAMORMYROPS SPHEKODES (SAUVAGE, 1879)

Mormyrops sphekodes Sauvage, 1879: 101. Lectotype: MNHN A 893, paralectotype: MNHN 1998-1050. Type locality: Ogooué River at Doumé, Gabon.
Mormyrops sphekodes – Sauvage, 1880: 55, Pl. 2, Fig. 4.
Mormyrus sphecodes – Günther, 1896: 280
Marcusenius sphecodes – Boulenger, 1898b: 793
Brienomyrus (Brienomyrus) sphecodes – Taverne, 1971: 106
Paramormyrops sphekodes – Hopkins *et al.*, 2007: 292–293 [Note: Hopkins *et al.* (2007: 304; fig. 12.65) erroneously illustrated *P. sphekodes* using the paralectotype rather than the lectotype. Both specimens are now regarded as the same species (see comparison with existing types, in the following text).]

Redescription of Paramormyrops sphekodes

Because of the confusion surrounding the identity of *P. sphekodes*, its rarity in our collections from Gabon, and the existence of only two historic specimens from the type locality, we redescribe this species based on the lectotype, paralectotype, four topotypes and five additional specimens from near the type locality.

Lectotype: MNHN A.893, 113.87 mm SL, male. Type location: Gabon, Ogooué-Lolo, Ogooué River at Doumé (modern GPS coordinates: 0.84137°S, 12.96548°E). A. Marche, late 1876–early 1877.

Paralectotype: MNHN 1998-1050, 96.7 mm SL, female. Type location: Gabon, same location and date as lectotype.

Topotypes (4): Rapids in front of the village of Doumé on the Ogooué River (0.84137°S, 12.96548°E): CUMV 96810 (1, specimen no. JPS-1118) 117.7 mm SL. J.P. Sullivan, 29 May 2011; MRAC B5-26-P-2 (1, specimen no. JPS-1192) 113.5 mm SL. J.P. Sullivan, 17 September 2014; AMNH 264378 (1, specimen no. JPS-1193) 94.5 mm SL. J.P. Sullivan, 17 September 2014; MNHN 2015-0257 (1, specimen no. JPS-1201) 111 mm SL. J.P. Sullivan, 17 September 2014.

Other specimens (5): Five specimens included here are from a site close to the type locality. Sébé River, 45 km south-east of Doumé, Ogooué-Lolo, Gabon (0.93442°S, 13.35777°E) J.P. Sullivan, 20 September 2014: MNHN 2015-0258 (1, specimen no. JPS-1214) male, 112.5 mm SL; AMNH 264377 (1, specimen no. JPS-1216) male, 110 mm SL; CUMV 98161 (1, specimen no. JPS-1219) female, 118.3 mm SL; MRAC B5-26-P-1 (1, specimen no. JPS-1230) male, 133 mm SL; 22 September 2014; CUMV 98177 (1, specimen no. JPS-1238), male, 119.5 mm SL.

Diagnosis: Paramormyrops sphekodes is distinguished from all other *Paramormyrops* by this combination of characters: 5 teeth in upper-jaw, 6 in lower; 12 circumpeduncular scales; sharp head profile, V-shaped when viewed from above; snout angle 48–56° corresponding to an interorbital width 1–1.36 times the snout length; BD 15.4–17.31% SL, BD at pectoral fin 84–94% BD at urogenital pore; eye diameter 13–16% HL measured from snout tip to posterior edge of bony operculum; snout length 24–27% HL; ratio of HL to depth (HLx/HDx, measured from radiographs) 1.1–1.24; HL 21–23% SL; EOD waveform with two phases, head-positive then negative, EOD duration 1.635 ± 0.226 ms with a corresponding power spectrum peak at 1573 ± 531 Hz; electric organ composed of type NPp electrocytes, that is having *N*on-*P*enetrating stalks innervated on the *p*osterior face of the cell (Hopkins, 1999).

Comparison with other Paramormyrops: With five teeth in the upper jaw and six in the lower, *P. sphekodes* differs from *P. hopkinsi, P. jacksoni* and *P. tavernei*, which have seven or more teeth in the upper jaw and eight or more in the lower jaw. With 12 circumpeduncular scales, it differs from *P. longicaudatus*, the undescribed species coded in Sullivan *et al.* (2002) as *P. sp. 'OFF', P. batesii* and *P. tavernei* which all have 16 or more. With its relatively sharp V-shaped head profile, *P. sphekodes* differs from *P. batesii*, *P. gabonensis, P. retrodorsalis, P. tavernei* and *P. kingsleyae* which have distinctly blunt or U-shaped snouts. *P. sphekodes* has type NPp electrocytes in its electric organ, as do seven other *Paramormyrops* from Lower Guinea, while *P. batesii* and *P. kingsleyae* have electric organs composed of electrocytes with penetrating stalks innervated on the anterior face (Type Pa). These characters are summarized in the key and in Fig. 16.

Paramormyrops sphekodes differs from *P. curvifrons* in head and snout shape. Head and shout are shorter, deeper and more rounded when viewed laterally in *P. sphekodes* compared to *P. curvifrons. P. curvifrons* also has a downward sloping forehead, protruding snout and enlarged chin. The ratio of HL to SL is 23.5–26.9 in *P. curvifrons*, higher than 21.5–23.4 in *P. sphekodes* (Fig. 5A, Table 2), while the ratio of HD to HL (external measurement using callipers) is reduced in *P. curvifrons* compared to *P. sphekodes* (Fig. 5C). The ratio of pre-pectoral distance to pre-dorsal distance is greater in *P. curvifrons* compared to *P. sphekodes* (Fig. 5B, Table

2), and *P. curvifrons* has a significantly narrower snout than *P. sphekodes* measured by either snout angle (Fig. 5G) or ratio IOW/SNL (Fig. 5D, Table 2).

Paramormyrops sphekodes is most easily confused with the species referred to above as SN4, but SN4 may be recognized by its much longer duration EOD, and by subtle morphometric characters discussed above and illustrated in Figs 3 and 4. Other distinguishing characters are presented below in the description of the new species.

Description: Based on the lectotype Fig. 1A (above) and 1B and 10 other specimens, Table 2. Figure 7 shows five specimens in photographs of live fish in the field.

A small-bodied *Paramormyrops*, the largest is a male, 133 mm SL, 153 mm TL. Body laterally compressed, maximum width at opercular bones. Viewed laterally, dorsal and ventral profile nearly parallel from behind the head to the first anal ray. Median BD 16.1% SL at pectoral fin, 17.6% SL at the urogenital pore. The ratio of these two BDs 84–89%, indicating that the depth changes little from anterior to posterior of the body anterior of the anal fin. Caudal peduncle length 17–20% SL, slightly wider at its origin than middle, depth 25–29% CPL. Lobes of caudal fin rounded.

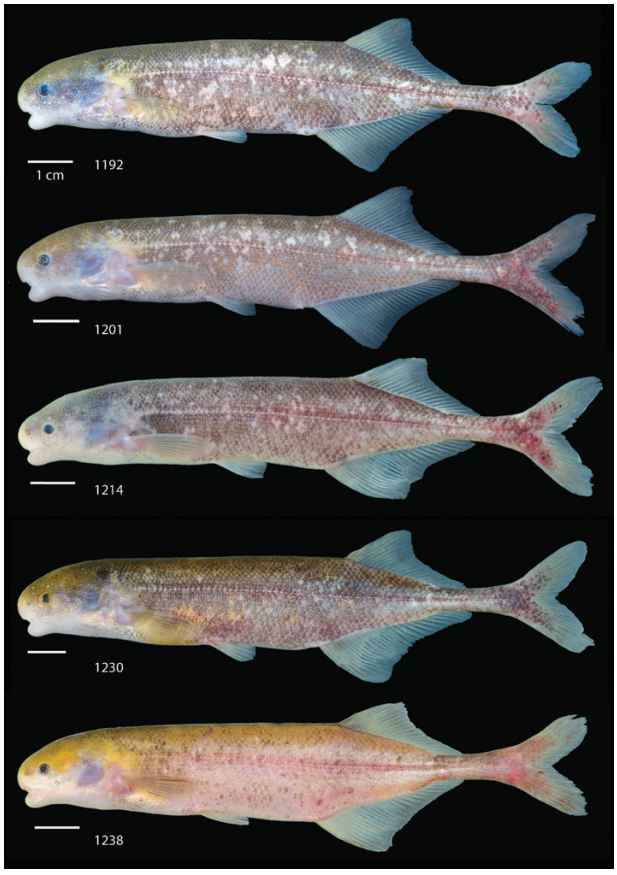

Figure 7. Five specimens of *P. sphekodes* from Ogooué basin of Gabon. From top to bottom: specimen tag number 1192, female, 113.5 mm; 1201, female, 111 mm from the Ogooué River at Doumé; 1214, male, 112.5 mm; 1230, male, 133 mm and 1238, male, 119 mm from the Sébé River nearby. Scale bars = 1 cm.

Lateral head profile above eye usually gently convex to very slightly concave in some individuals (Fig. 7, #1214). Snout short and smoothly rounded (Fig. 7). Forehead downward-sloping from halfway between opercular opening and snout tip. Tip of the snout one half eye diameter below the ventral margin of the eye. Viewed dorsally, head and snout V-shaped or sharp, median snout angle 53.6°, less sharp than *P. curvifrons* (Fig. 5D).

Mouth small, rictus directly beneath nares. Chin protrudes slightly below gular region, not extending beyond snout. Eye small, ED 11–14% HL, positioned mid-laterally. Eye socket forms pale ring around pigmented eye, with gold iris and dark centre. IOW 26.8–29.3% HL. Anterior naris about 1/3 distance from snout tip to eye, slightly below line drawn through centre of eye, posterior naris halfway between anterior naris and eye, at about level of eye's lower margin. Opercular opening begins anterior to base of pectoral fin. POL 60–68% HL.

Pectoral-fin origin beneath posterior terminus of opercular opening, slightly below mid-horizontal line, length 12.4–17.0% SL, 11 rays. Pelvic-fin origin at 35.0–38.8% SL, length 9.2–10.8% SL, positioned ventrally, 6 rays. Dorsal-fin origin at 64–65% SL; anterior margin gently convex, trailing margin concave in first third, remainder levels off at ½ DFH. Maximum height 62.3–79.2% DFL, 20–23 total rays. Anal-fin origin slightly anterior to dorsal-fin origin: dorsal-fin origin above seventh (fifth branched) anal-fin ray. Anal fin mirrors general shape of dorsal fin, maximum height 45.2–65.0% AFL. In males, anterior AFR thickened and stiff with a noticeable notch at the base of the anal fin, spanning anterior half of anal-fin base. End of anal-fin base terminus directly beneath end of dorsal-fin base, rays 24–28. Lobes of caudal fin rounded, equal, slightly wider than caudal peduncle, deeply cleft, scaled at their bases.

Scales fine, cycloid, absent from head. Pierced lateral line scales, 63–68 based on recent specimens (lectotype = 72, significantly fewer than Sauvage's description of 85 which must have been total scales rather than pierced scales). Our counts of lateral line scales on the lectotype are unreliable because of damage to the specimen, other counts and measurements for the lectotype are indicated separately from other specimens in Table 2. Scales between lateral line and anterior base of dorsal fin 9–11, 10–15 scale rows between pelvic fin and lateral line. Circumpeduncular scales 12. Vertebrae: 43–45 total, 18–19 precaudal, 24–26 caudal. Teeth bicuspid, 5 in upper, 6 in lower jaw.

Coloration: All fins with lightly pigmented rays, membranes hyaline. Dark band absent between dorsal

and anal fins. Body darker dorsally, lighter ventrally. When alive, tan-brown body with yellow-olive or golden accents on top of head, back, and belly. Mouth, chin, and gular region unpigmented, whitish. Many small unpigmented spots and pores over electroreceptors (mormyromast and ampullary organs) visible on top of head and back, with fewer, large white spots (knollenorgans) on head. Preserved specimens uniform greyish-brown.

Electric organ discharge: Short biphasic pulses – head positive first then head negative – average duration, 0.851 ± 0.352 ms (Fig. 8A, C, Table 3). First positive peak, P1, width W1 0.519 ± 0.194 ms (range: 0.320–0.940 ms) – 1.6 times longer than width W2. First-time derivative of EOD rises smoothly from baseline with a single peak before P1 (Fig. 8B). Power spectrum of EOD peaks at 1910 ± 540 Hz (n = 9, Table 3, Fig. 10 D, E). Other quantitative measurements of EODs are summarized in Table 3 using reference landmarks illustrated for the biphasic EOD in Fig. 8A and its power spectrum in Fig. 8D.

Several other species of *Paramormyrops* with biphasic EODs possess electric organs composed of electrocytes with *N*on-*P*enetrating stalks that are innervated on the *p*osterior faces of each cell (Type NPp Bennett, 1971; Bass, 1986; Sullivan *et al.*, 2000; Gallant *et al.*, 2011). Other species in this and other genera produce triphasic EODs (three peaks), beginning with a small head-negative phase P0, in advance of the larger head-positive phase P1, and the final head-negative phase P2. In all species with triphasic EODs, the electric organs are composed of electrocytes with *P*enetrating stalks innervated on the *a*nterior face of each cell (Type Pa in Alves-Gomes & Hopkins 1997). Inspection of the EODs of all *P. sphekodes* reveals that the P0 peak is absent, even when the discharge trace is expanded 20 times by amplification (Fig. 8A, thin trace), suggesting that the electric organ is composed of Type NPp electrocytes. This is confirmed by dissection and histology shown in Fig. 9.

Like many other mormyrids, *P. sphekodes* exhibits a sex difference in EOD waveform duration. One male recorded near the end of the rainy season in May 2011 had the longest EODs in all our EOD recordings (1.60 ms), but other, smaller males recorded early in the rainy season of September 2014 had EODs more similar to those of females. The averages of male and female EOD durations do not differ significantly (Student's t = 1.439, d.f. = 7, P = 0.19, Table 3). In all adult males with *SL* > 115 mm, we note that the ratio of the width of the second peak, W2, to total duration, DT, is greater than for that for females (Student's t = 2.99, P = 0.03). The ratio of W1 to DT is correspondingly less for males. The variation seen for male EODs might be a reflection of seasonal changes in male pulses which begin to elongate before or shortly after the onset of the rains when most mormyrids breed (Hopkins, 1980, 1981; Hopkins & Bass, 1981; Bass & Hopkins, 1983, 1985).

Distribution. In spite of several previous collecting trips to the lower, middle and upper Ogooué River of Gabon in 1999, 2001 and 2002, our only collections of this species are from Doumé, the type locality (2011, 2014), and the Sébé River, about 45 km from Doumé (2014). Both sites are within the Ogooué-Lolo Province of Gabon (Fig. 10) and both are large river habitats with rocky bottoms, sandy substrate, with rushing water and rapids (Fig. 11); this species was absent from nearby streams and other smaller tributaries.

Etymology: The name *sphekodes* comes from the Greek, σφήκα, for wasp, which may refer to the fish's elongate and slender body (Harder, 2000); however, Sauvage (1879, 1880) gives no explanation for his name for this species.

The specimens referred to as 'SN4' above and in Sullivan et al. (2002, 2004) are here described as a new species.

PARAMORMYROPS NTOTOM SP. NOV.
(FIG. 12, TABLE 2)

urn:lsid:zoobank.org:act:7BD331A4-1E58-4420-91D9-DA197125340B

Holotype: CUMV 98138, 175 mm SL, male, tag number JPS-1189, Gabon, Ogooué-Lolo, Ogooué River at Doumé, GPS coordinates: 0.84137°S, 12.96548°E, J.P. Sullivan & B. Sidlauskas, 17 September 2014.

Paratypes (22): Ogooué River at Doumé (10) (0.843°S, 12.96°E): J.P. Sullivan, 29 May 2011: CUMV 96811, JPS-1117, 120 mm SL; AMNH 264795, formerly CUMV 96811, JPS-1119, 110 mm SL; MNHN 2016-0016, formerly CUMV 96811, JPS-1120, 152 mm SL; MRAC 2016-010-P-00001, formerly CUMV 96811, JPS-1122, 162 mm SL. (–0.841, 12.965): J.P. Sullivan & B. Sidlauskas, 17 September 2014: CUMV 98129, JPS-1179, 121.5 mm SL; AMNH 264796, formerly CUMV 98132, JPS-1183, 126 mm SL; MNHN 2016-0017, formerly CUMV 98133, JPS-1184, 125.5 mm SL; MRAC 2016-010-P-00002, formerly CUMV 98141, JPS-1198, 137 mm SL; CUMV 98142, JPS-1199, 137.5 mm SL; AMNH 264797, formerly CUMV 98144, JPS-1202,133 mm SL.
Upper Ogooué River (12) Under bridge near Franceville (1.637°S, 13.530°E) C.D. Hopkins et al., 7 August 1999. (9): AMNH 264798, formerly CUMV 80463, tag no. 3465, 7 August 1999; MNHN 2016-0018, formerly CUMV 80463, tag no. 3466, 132 mm SL; MRAC 2016-010-P-00003, formerly CUMV 80463, tag no. 3467, 157 mm; CUMV 96850 (6, specimen nos. JPS-1095, JPS-1099 = AMNH 264799 JPS-1102, JPS-1103, JPS-1104, JPS-1105) 116–137 mm SL, J.P. Sullivan, 27 May 2011.

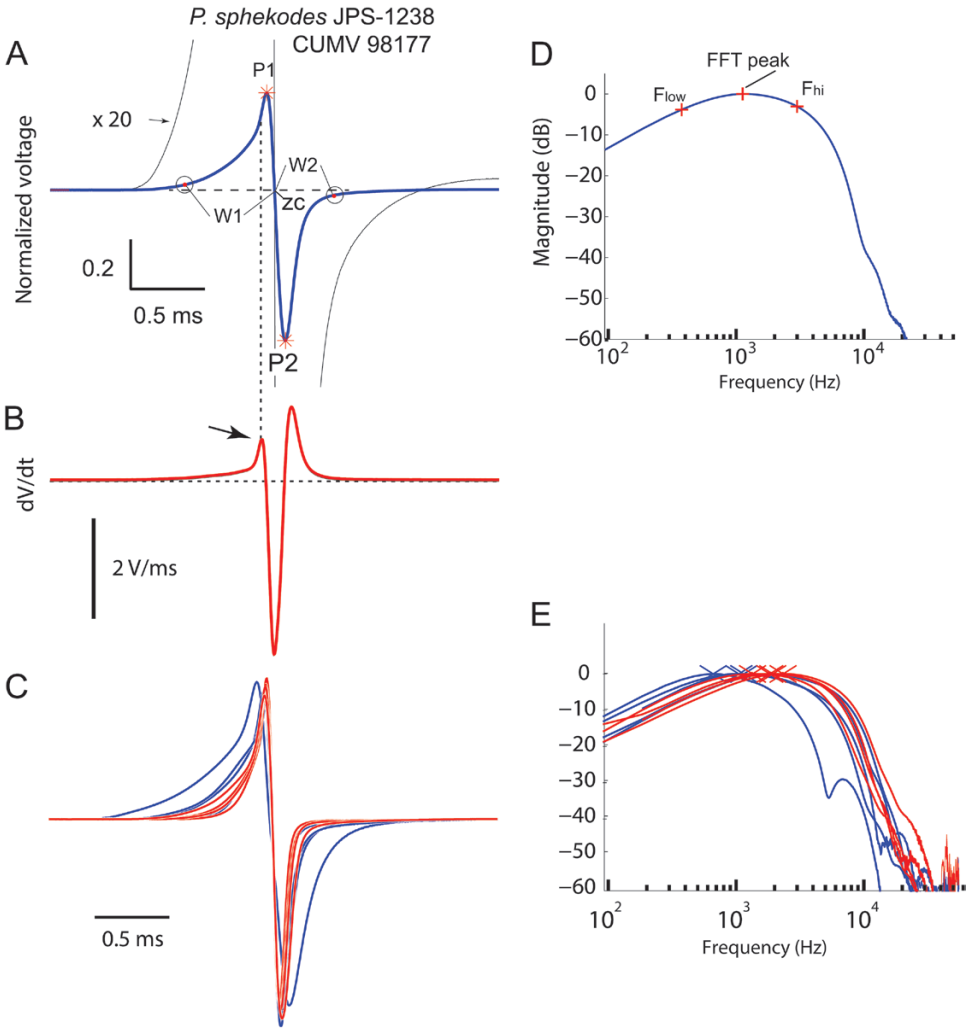

Figure 8. Electric organ discharges (EODs) from *P. sphekodes*. (A) *Paramormyrops sphekodes* specimen CUMV 98177 (tag JPS-1238), a male from type locality showing normalized voltage as a function of time, that is 1.0 V peak-to-peak. Head positivity is upwards on all traces. There are two peaks to the waveform: P1, which is head-positive, and P2, which is head-negative. EOD duration is measured between points marked by open circles – the first and last points exceed ±0.02 V. W1 and W2 are the widths of the first and second peaks. The thin line is a 20× vertical expansion of the waveform which rises gradually from the baseline with no indication of a head-negative pre-pulse, P0, that is present in some other species. The final overshoot, due to AC-coupling of the amplifier, is absent when making DC-coupled recordings. The dashed line indicates the zero baseline. (B) Time derivative, *dV/dt,* of EOD waveform in (A) has a single positive peak (arrow) in advance of peak P1 and there is no inflection point on the rising phase before P1. (C) EODs from nine specimens of *P. sphekodes* showing the stereotypy of the species waveform. After normalization to unity peak-to-peak height, all EODs are centred on the zero-crossing between P1 and P2 [zc in (A)]. Males are plotted in blue and females are plotted in red. (D) Power spectral density of EODs of *P. sphekodes* in (A) with its maximum power at 1125 Hz. F_{low} and F_{hi} are the frequencies where the spectral power drops 3 dB below the peak power of the FFT. The bandwidth of the power spectrum is F_{hi}–F_{low}. (E) Superimposed power spectra for the nine EODs shown in (C) with peak frequencies marked with 'x'. Axes units are as in D.

Ogooué River, 30 minutes downriver from bridge near Franceville (1.603°S, 13.529°E): 14 August 1999. (3); MNHN 2016-0020, formerly CUMV 80507, tag no. 3667, 157 mm SL.; CUMV 80507, tag no. 3671, 187 mm SL; CUMV 80507, tag no. 3720, 139 mm SL.

Non-type specimens used for phylogenetic analysis: Okano River near Mitzig (0.80983°N, 11.64633°E): AMNH 231500 (specimen no. 4149, referred to as *B.* cf. *curvifrons* in Sullivan *et al.*, 2004), J.P. Sullivan *et al.*, 2001-08-17.

Table 3. Electric organ discharge waveform measurements for three species of *Paramormyrops*

	P. sphekodes						***P. ntotom* sp. nov.**								***P. curvifrons***					
	Topotypes + other specimens						Holotype	Paratypes + others (n = 44)							Topotypes					
	Female		Male		Combined			Females/Juv		Male		Combined			Females		Males		Combined	
	$n = 4$		$n = 5$		$n = 9$			$n = 16$		$n = 28$		$n = 44$			$n = 4$		$n = 10$		$n = 14$	
	Mean	SD	Mean	SD	Mean	SD		Mean	SD	Mean	SD	Mean	SD		Mean	SD	Mean	SD	Mean	SD
Total duration (ms)	0.673	0.157	0.993	0.416	0.851	0.352	5.813	3.983	0.676	5.248	1.031	4.788	1.098		2.715	0.369	3.471	0.761	3.255	0.747
W1 (ms)	0.433	0.103	0.588	0.232	0.519	0.194	2.880	1.920	0.282	2.398	0.403	2.225	0.429		1.408	0.179	1.639	0.256	1.573	0.254
W2 (ms)	0.240	0.055	0.404	0.185	0.331	0.152	2.933	2.063	0.419	2.850	0.698	2.564	0.717		1.307	0.239	1.832	0.568	1.682	0.055
Voltage P1 (V)	0.411	0.022	0.395	0.024	0.402	0.023	0.375	0.361	0.032	0.358	0.035	0.359	0.034		0.385	0.048	0.367	0.031	0.372	0.035
Voltage P2 (V)	−0.589	0.022	−0.605	0.024	−0.598	0.023	−0.625	−0.639	0.032	−0.642	0.035	−0.641	0.034		−0.615	0.048	−0.633	0.031	−0.628	0.035
W1/TD	0.643	0.010	0.598	0.032	0.618	0.033	0.375	0.484	0.026	0.461	0.040	0.469	0.037		0.520	0.039	0.479	0.052	0.491	0.051
W2/TD	0.357	0.010	0.402	0.032	0.382	0.033	0.505	0.516	0.026	0.539	0.040	0.531	0.037		0.480	0.039	0.521	0.052	0.509	0.051
W1/W2	1.803	0.082	1.500	0.214	1.635	0.226	0.982	0.943	0.098	0.865	0.142	0.893	0.934		1.094	0.168	0.938	0.184	0.982	0.188
|vP1/vP2|	0.699	0.062	0.654	0.065	0.674	0.064	0.599	0.568	0.076	0.562	0.082	0.564	0.079		0.633	0.131	0.583	0.075	0.598	0.092
FFT peak (Hz)	1910	360	1303	531	1573	540	188	308	57	241	61	265	67		410	70	366	82	378	79

Table 4. List of specimens referenced in this study, along with specimen tag numbers, museum numbers, Macaulay Library numbers, GenBank numbers, year of collection, sex, standard length and general location of collection

Specimens (n = 95)	Type status	Tag no.	Museum no.	Macaulay no.	GenBank no.	Year collected	Sex	SL (mm)	Location
Paramormyrops curvifrons	Holotype	None	MRAC 75-24-P-132	None		1974	M	107.35	Ivindo
Paramormyrops curvifrons		1367	CUMV 75407	511585		1994	M	127.03	Ivindo
Paramormyrops curvifrons		1426	CUMV 75408	511588		1994	M	98.15	Ivindo
Paramormyrops curvifrons		1434	CUMV 75409	511589		1994	M	106.03	Ivindo
Paramormyrops curvifrons		1440	CUMV 75409	511591		1994	F	101.01	Ivindo
Paramormyrops curvifrons		1441	CUMV 75409	511592		1994	M	116.63	Ivindo
Paramormyrops curvifrons		1442	CUMV 75409	511593		1994	M	123.76	Ivindo
Paramormyrops curvifrons		1443	CUMV 75409	511594		1994	M	103.95	Ivindo
Paramormyrops curvifrons		1444	CUMV 75409	511595		1994	M	112.23	Ivindo
Paramormyrops curvifrons		1446	CUMV 75410	511596		1994	M	113.04	Ivindo
Paramormyrops curvifrons		1447	CUMV 75410	511597		1994	F	84.58	Ivindo
Paramormyrops curvifrons		1448	CUMV 75410	511598		1994	F	88.49	Ivindo
Paramormyrops curvifrons		1449	CUMV 75410	511599		1994	F	93.02	Ivindo
Paramormyrops curvifrons		1450	CUMV 75410	511600		1994	M	104.11	Ivindo
Paramormyrops curvifrons		1451	CUMV 75410	511601		1994	M	101.23	Ivindo
Paramormyrops curvifrons		1452	CUMV 75410	511602		1994	F	76.91	Ivindo
Paramormyrops curvifrons		1395	CUMV 75411	511655		1994	M	118.04	Ivindo
Paramormyrops curvifrons		1036	CUMV 75449	511604		1993	M	111.31	Ivindo
Paramormyrops curvifrons		1039	CUMV 75449	511605		1993	F	91.86	Ivindo
Paramormyrops curvifrons		1042	CUMV 75449	511606		1993	M	118.65	Ivindo
Paramormyrops curvifrons		1043	CUMV 75449	511607		1993	F	103.67	Ivindo
Paramormyrops curvifrons		1045	CUMV 75449	511608		1993	F	104.31	Ivindo
Paramormyrops curvifrons		2050	CUMV 81661	511573	AF477469	1998			Ivindo
Paramormyrops curvifrons		JPS-1002	CUMV 96847	197349		2011	M	122	Ivindo
Paramormyrops curvifrons		JPS-1003	CUMV 96847	197350		2011	M	116	Ivindo

Table 4. Continued

Specimens (n = 95)	Type status	Tag no.	Museum no.	Macaulay no.	GenBank no.	Year collected	Sex	SL (mm)	Location
Paramormyrops curvifrons		JPS-1006	CUMV 96847	197351		2011	M	107	Ivindo
Paramormyrops curvifrons		JPS-1007	CUMV 96847	197352		2011	M	82.5	Ivindo
Paramormyrops curvifrons		JPS-1009	CUMV 96847	197353		2011	M	137	Ivindo
Paramormyrops curvifrons		JPS-1017	CUMV 96847	197354		2011	M	119	Ivindo
Paramormyrops curvifrons		JPS-1018	CUMV 96847	197355		2011			Ivindo
Paramormyrops curvifrons		JPS-1021	CUMV 96847	197356		2011	M	111	Ivindo
Paramormyrops curvifrons		JPS-1023	CUMV 96847	197357		2011	M	126	Ivindo
Paramormyrops curvifrons		JPS-1027	CUMV 96847	197358		2011	M	147	Ivindo
Paramormyrops curvifrons		JPS-1031	CUMV 96847	197359		2011	M	139	Ivindo
Paramormyrops curvifrons		JPS-1041	CUMV 96847	197360		2011	M	114.5	Ivindo
Paramormyrops curvifrons		JPS-1049	CUMV 96847	197361		2011	M	117	Ivindo
Paramormyrops curvifrons		JPS-1066	CUMV 96847	197362		2011	M	124.5	Ivindo
Paramormyrops curvifrons		None	MRAC 73-29-0-639	None		1970	M	140.61	Ivindo
***Paramormyrops ntotom* sp. nov.**	Holotype	JPS-1189	CUMV 98138	197470	KT369077, KX886810	2014	M	178	Ogooué
***Paramormyrops ntotom* sp. nov.**	Paratype	3465	CUMV 80463	51364		1999	M	171.8	Ogooué
***Paramormyrops ntotom* sp. nov.**	Paratype	3466	CUMV 80463	51365		1999	F	125.55	Ogooué
***Paramormyrops ntotom* sp. nov.**	Paratype	3467	CUMV 80463	51366		1999	F	125.68	Ogooué
***Paramormyrops ntotom* sp. nov.**	Paratype	3667	CUMV 80507	513185		1999	M	149.78	Ogooué
***Paramormyrops ntotom* sp. nov.**	Paratype	3671	CUMV 80507	513187		1999	M	183	Ogooué
***Paramormyrops ntotom* sp. nov.**	Paratype	3720	CUMV 80507	513227		1999	M	137	Ogooué
***Paramormyrops ntotom* sp. nov.**	Paratype	JPS-1117	CUMV 96811	197303	KT369072	2011	F	117.16	Ogooué
***Paramormyrops ntotom* sp. nov.**	Paratype	JPS-1119	CUMV 96811	197304	KT369073	2011	F	107.79	Ogooué
***Paramormyrops ntotom* sp. nov.**	Paratype	JPS-1120	CUMV 96811	197305	KT369074	2011	M	148.36	Ogooué
***Paramormyrops ntotom* sp. nov.**	Paratype	JPS-1122	CUMV 96811	197306	KT369075	2011	M	157.91	Ogooué
***Paramormyrops ntotom* sp. nov.**	Paratype	JPS-1095	CUMV 96850	197384		2011	F	124.5	Ogooué
***Paramormyrops ntotom* sp. nov.**	Paratype	JPS-1099	CUMV 96850	197386	KT369071	2011	F	116	Ogooué

Table 4. Continued

Specimens (n = 95)	Type status	Tag no.	Museum no.	Macaulay no.	GenBank no.	Year collected	Sex	SL (mm)	Location
***Paramormyrops ntotom* sp. nov.**	Paratype	JPS-1102	CUMV 96850	197388		2011	F	119	Ogooué
***Paramormyrops ntotom* sp. nov.**	Paratype	JPS-1103	CUMV 96850	197389		2011	F	137	Ogooué
***Paramormyrops ntotom* sp. nov.**	Paratype	JPS-1104	CUMV 96850	197390		2011	F	130	Ogooué
***Paramormyrops ntotom* sp. nov.**	Paratype	JPS-1105	CUMV 96850	197391		2011	F	117	Ogooué
***Paramormyrops ntotom* sp. nov.**	Paratype	JPS-1183	CUMV 98132	197464		2014	M	126	Ogooué
***Paramormyrops ntotom* sp. nov.**	Paratype	JPS-1184	CUMV 98133	197465		2014	M	125.5	Ogooué
***Paramormyrops ntotom* sp. nov.**	Paratype	JPS-1198	CUMV 98141	197479		2014	M	137	Ogooué
***Paramormyrops ntotom* sp. nov.**	Paratype	JPS-1199	CUMV 98142	197480		2014	F	137.5	Ogooué
***Paramormyrops ntotom* sp. nov.**	Paratype	JPS-1202	CUMV 98144	197483		2014	M	133	Ogooué
***Paramormyrops ntotom* sp. nov.**	Paratype	JPS-1179	CUMV98129	197460		2014	F	121.5	Ogooué
***Paramormyrops ntotom* sp. nov.**		4149	AMNH 231500	513132	AY475209	2001			Okano
***Paramormyrops ntotom* sp. nov.**		3396	CUMV 80458	513160	KT369080	1999	F	111.4	Ogooué
***Paramormyrops ntotom* sp. nov.**		3465	CUMV 80463	513164	KT369081	1999	M	170	Ogooué
***Paramormyrops ntotom* sp. nov.**		1844	CUMV 80591	513241	AF477439	1999	M	202	Ogooué
***Paramormyrops ntotom* sp. nov.**		JPS-1241	CUMV 98077	197518		2014	F	136	Sébé
***Paramormyrops ntotom* sp. nov.**		JPS-1244	CUMV 98078	197521		2014	F	141	Sébé
***Paramormyrops ntotom* sp. nov.**		JPS-1245	CUMV 98079	197522		2014	M	146	Sébé
***Paramormyrops ntotom* sp. nov.**		JPS-1242	CUMV 98080	197519	KT369079, KX886812	2014	F	133	Sébé
***Paramormyrops ntotom* sp. nov.**		JPS-1243	CUMV 98081	197520		2014	M	146	Sébé
***Paramormyrops ntotom* sp. nov.**		JPS-1222	CUMV 98086	197499		2014	F	122	Sébé
***Paramormyrops ntotom* sp. nov.**		JPS-1224	CUMV 98087	197501		2014	M	135	Sébé
***Paramormyrops ntotom* sp. nov.**		JPS-1225	CUMV 98088	197502		2014	F	147	Sébé
***Paramormyrops ntotom* sp. nov.**		JPS-1228	CUMV 98089	197505	KT369078, KX886811	2014	F	152	Sébé
***Paramormyrops ntotom* sp. nov.**		JPS-1229	CUMV 98090	197506		2014	M	177	Sébé
***Paramormyrops ntotom* sp. nov.**		JPS-1175	CUMV 98091	197456		2014	M	130	Ogooué
***Paramormyrops ntotom* sp. nov.**		JPS-1176	CUMV 98092	197457	KT369076, KX886809	2014	M	154	Ogooué

Table 4. Continued

Specimens (n = 95)	Type status	Tag no.	Museum no.	Macaulay no.	GenBank no.	Year collected	Sex	SL (mm)	Location
***Paramormyrops ntotom* sp. nov.**		JPS-1177	CUMV 98127	197458		2014	M	162	Ogooué
***Paramormyrops ntotom* sp. nov.**		JPS-1178	CUMV 98128	197459		2014	M	147	Ogooué
***Paramormyrops ntotom* sp. nov.**		JPS-1181	CUMV 98130	197462		2014	F	132	Ogooué
***Paramormyrops ntotom* sp. nov.**		JPS-1182	CUMV 98131	197463		2014	M	163	Ogooué
***Paramormyrops ntotom* sp. nov.**		JPS-1185	CUMV 98134	197466		2014	M	176	Ogooué
***Paramormyrops ntotom* sp. nov.**		JPS-1186	CUMV 98135	197467		2014	M	162	Ogooué
***Paramormyrops ntotom* sp. nov.**		JPS-1187	CUMV 98136	197468		2014	M	165	Ogooué
***Paramormyrops ntotom* sp. nov.**		JPS-1188	CUMV 98137	197469		2014	F	144	Ogooué
***Paramormyrops ntotom* sp. nov.**		JPS-1191	CUMV 98139	197472		2014	F	116	Ogooué
***Paramormyrops ntotom* sp. nov.**		JPS-1197	CUMV 98140	197478		2014	F	145	Ogooué
***Paramormyrops ntotom* sp. nov.**		JPS-1200	CUMV 98143	197481		2014	M	150	Ogooué
***Paramormyrops ntotom* sp. nov.**		JPS-1217	CUMV 98261	197494		2014	M	111	Sébé
Paramormyrops sphekodes	Lectotype	A893	MNHN A893	None		1876–1877	M	113.87	Ogooué
Paramormyrops sphekodes	Paralectotype	None	MNHN 1998-1050	None		1876–1877	F	98.67	Ogooué
Paramormyrops sphekodes	Topotype	JPS-1193	AMNH264378	197474	KT369084, KX886814	2014	F	94.5	Ogooué
Paramormyrops sphekodes	Topotype	JPS-1118	CUMV 96810	197302	KT369082	2011	M	117.69	Ogooué
Paramormyrops sphekodes	Topotype	JPS-1201	MNHN 2015-0257	197482	KT369085, KX886815	2014	F	111	Ogooué
Paramormyrops sphekodes	Topotype	JPS-1192	MRAC B5-26-P-2	197473	KT369083, KX886813	2014	F	113.5	Ogooué
Paramormyrops sphekodes		JPS-1216	AMNH264377	197493	KT369087	2014	M	110	Sébé
Paramormyrops sphekodes		JPS-1219	CUMV 98161	197496	KT369088	2014	F	118.3	Sébé
Paramormyrops sphekodes		JPS-1214	MNHN 2015-0258	197491	KT369086, KX886816	2014	M	112.5	Sébé
Paramormyrops sphekodes		JPS-1230	MRAC B5-26-P-1	197507	KT369089	2014	M	133	Sébé
Paramormyrops sphekodes		JPS-1238	CUMV 98177	197515	KT369090	2014	M	119.5	Sébé

Non-type specimens used for analysis of EODs: Doumé rapids, left bank of Ogooué River (0.841° S, 12.965° E): J.P. Sullivan, 16 September 2014: CUMV 98092 (1, specimen no. JPS-1176) 154 mm SL, EOD no. 197457. J.P. Sullivan, 17 September 2014: CUMV 98127 (1, specimen no. JPS-1177) 162 mm SL, EOD no. 197458. CUMV 98128 (1, specimen no. JPS-1178) 147 mm SL, EOD no. 197459. CUMV

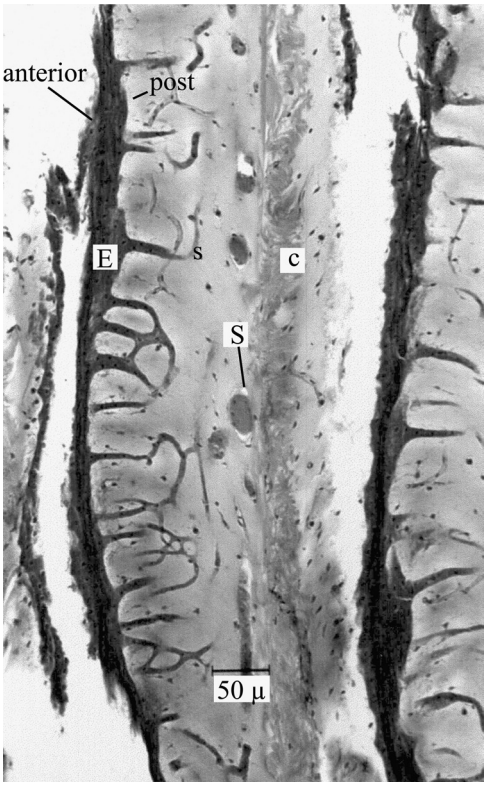

Figure 9. Histology of para-sagittal section of paralectotype of *P. sphekodes* specimen MNHN 1998-1050 (Female, 98.7 mm, SL) shows electrocytes of type NPp (*N*on-*P*enetrating stalks with *p*osterior innervation). The specimen, collected from Doumé Falls by Alfred Marche in 1876–1877 and preserved in alcohol, was embedded in plastic, sectioned with a tungsten carbide knife at 7 µm and stained with toluidine blue. E = main body of the electrocyte; anterior = anterior face of electrocyte; post = posterior face of same electrocyte; c = collagen layer separating two electrocytes; S = stalk of electrocyte which is innervated by the axons from the electromotor nerve (not shown); s = stalklets, or small branches from a dividing stalk that eventually fuse with posterior face of the electrocyte. Stalks are innervated on the posterior side of the electrocyte and all branches of the stalk system remain posterior to the main body of the electrocyte without crossing to the opposite or anterior side.

98130 (1, specimen no. JPS-1182) 132 mm SL, EOD no. 197462. CUMV 98131 (1, specimen no. JPS-1182) 163 mm SL, EOD no. 197463. CUMV 98134 (1, specimen no. JPS-1185) 176 mm SL, EOD no. 197466. CUMV 98135 (1, specimen no. JPS-1186) 162 mm SL, EOD no. 197467. CUMV 98136 (1, specimen no. JPS-1187) 165 mm SL, EOD no. 197468. CUMV 98137 (1, specimen no. JPS-1188) 144 mm SL, EOD no. 197469. CUMV 98139 (1, specimen no. JPS-1191) 116 mm SL, EOD no. 197472. CUMV 98140 (1, specimen no. JPS-1197) 145 mm SL, EOD no. 197478. CUMV 98143 (1, specimen no. JPS-1200) 150 mm SL, EOD no. 197481.

Sébé River, left bank rocks below bridge (0.93442°S, 13.35777°E): J.P. Sullivan, 20 September 2014: CUMV 98261 (1, specimen no. JPS-1217) 111 mm SL, EOD no. 197494. CUMV 98086 (1, specimen no. JPS-1222) 122 mm SL, EOD no. 197499. CUMV 98087 (1, specimen no. JPS-1224) 135 mm SL, EOD no. 197501. CUMV 98088 (1, specimen no. JPS-1225) 147 mm SL, EOD no. 197502. CUMV 98089 (1, specimen no. JPS-1228) 152 mm SL, EOD no. 197505. CUMV 98090 (1, specimen no. JPS-1229) 177 mm SL, EOD no. 197506. J.P. Sullivan, 22 September 2014: CUMV 98077 (1, specimen no. JPS-1241) 136 mm SL, EOD no. 197518. CUMV 98080 (1, specimen no. JPS-1242) 133 mm SL, EOD no. 197519. CUMV 98081 (1, specimen no. JPS-1243) 146 mm SL, EOD no. 197520. CUMV 98078 (1, specimen no. JPS-1244) 141 mm SL, EOD no. 197521. CUMV 98079 (1, specimen no. JPS-1245) 146 mm SL, EOD no. 197522.

Diagnosis: Paramormyrops ntotom sp. nov. is distinguished from all other Lower-Guinea *Paramormyrops* by a combination of morphological and electrical characteristics: 5 teeth in upper-jaw, 6 in lower; 12 circumpeduncular scales; 'V'-shaped snout profile viewed from above, snout angle 38–50° (Fig. 5D), corresponding to an interorbital width 0.8–1.05 times the snout length; BD 14.9–18.1% SL, 81–91.6% of BD at urogenital pore (Fig. 5E); eye diameter 12.4–14.7% HL measured to end of opercular bone (Fig. 5F); snout length 23.8–28.3% HL; ratio of HL to depth (HLx/HDx measured from radiographs) 1.25–1.40 (Fig. 4A); HL 20.4–24.6% SL; EOD waveform with two phases, head positive then negative, duration 4.78 ± 1.10 ms with a corresponding peak power spectral frequency, 265 ± 67 Hz; electric organ composed of type NPp electrocytes (Sullivan *et al.*, 2002).

Comparison with other Paramormyrops*:* With its 5/6 teeth, 12 circumpeduncular scales and sharp snouts, *P. ntotom* sp. nov. differs from all other described *Paramormyrops* except *P. curvifrons* and *P. sphekodes*. We treat both of these in turn.

Four morphological characters distinguish *P. ntotom* sp. nov. from *P. curvifrons*. (1) ratio of HL to SL shorter in *P. ntotom* sp. nov. compared with *P. curvifrons* (Fig. 5A); (2) slight concave depression in the forehead in advance of the orbit and a relatively compact snout compared to *P. curvifrons* which has a longer snout, downward sloping, often with a slightly protruding chin and upper lip; (3) shorter prepectoral distance relative to predorsal distance (Fig. 5B); (3) snout angle greater in *P. ntotom* sp. nov. than *P. curvifrons* (Fig. 5D, G) and (4) the HD relative to HL greater in *P. ntotom* sp. nov. than *P. curvifrons* (Fig. 5C).

Figure 10. Distribution map of West-Central Africa showing collection localities of specimens of *P. sphekodes* (blue), ***P. ntotom* sp. nov.** (red) and *P. curvifrons* (green). Stars mark collection locations of holotypes (or lectotype) and circles mark locations of other specimens.

EOD duration slightly longer in *P. ntotom* sp. nov. compared with *P. curvifrons*, with extensive overlap (Fig. 15). Both species have type NPp electrocytes in the electric organ and both exhibit sex differences in EOD duration (Table 3, Fig. 15). Although these two species have overlapping EOD types, our collections indicate they are not anywhere sympatric. *Paramormyrops curvifrons* is known only from the Ivindo River in Gabon, while *P. ntotom* sp. nov. is known only from the Ogooué (Fig. 10).

Paramormyrops ntotom sp. nov. differs from *P. sphekodes* in the six following morphological characters: (1) larger overall size at sexual maturity (Fig. 2); (2) head more elongate and less rounded (Fig. 4); (3) snout reduced (Fig. 3, Fig. 5G); (4) larger caudal peduncle depth to length ratio (Fig. 3, Table 2); (5) the smaller eye diameter relative to HL, HLBO (Fig. 5F, Table 2); and (6) the greater EOD duration (Figs 2, 14).

When alive, *P. ntotom* sp. nov. is most easily distinguished from *P. sphekodes* by its longer EOD duration and a correspondingly lower peak spectral frequency (Table 3, Figs 8, 14, 15). The EODs of *P. ntotom* sp. nov. and *P. sphekodes* also differ in shape, with the width of first and second phase being equal for *P. ntotom* sp. nov., while W1 is longer than W2 in *P. sphekodes* (Fig. 15). Living specimens of these two species also differ in coloration. Dorsal and anal fin pigmentation tends to be darker in *P. ntotom* sp. nov. than *P. sphekodes*, and the ground color of the skin tends to be darker chocolate brown compared to yellow brown in *P. sphekodes* (Fig. 7).

Description: Photos and radiograph of the holotype are shown in Fig. 12. Table 2 summarizes morphometric ratios and meristics for it and 22 paratypes. Figure 13 shows five live specimens photographed in the field.

A large-bodied *Paramormyrops*, largest female, 137.5 mm SL (CUMV 98142, #JPS-1199), the largest male, 183 mm SL (CUMV 80507, #3671). Body laterally compressed with maximum width at opercular bones, 8.43–10.42% SL. Viewed laterally, BD increases gradually from base of the pectoral fin to its maximum at origin of the anal fin. BD at pectoral fin, 14.9–18.1% SL, BD at urogenital pore (BDUGP) 16.7–21.5% SL: the ratio of these two depths, 0.819–0.916, reflects the slight increase posteriorly compared to *P. sphekodes* (Table 2). BD decreases from origin of dorsal and anal fins to caudal peduncle. Caudal peduncle length 15.8–19.4% SL, slightly deeper at origin than centre, CPD 26.1–33.7% CPL. Lobes of caudal fin rounded.

Figure 11. (A, B) Collection localities near the rapids at Doumé (0.84245°S, +12.96249°E) on the Ogooué River of Gabon, where *P. sphekodes* is sympatric with ***P. ntotom* sp. nov.** (B) shows local villagers fishing with hoop nets at Doumé. (C, D) View of the Sébé River (0.93494°S, 13.35767°E) where the two species are also sympatric. Both habitats are moderate-sized rivers with gentle flow or rapids over rocky outcroppings, interspersed with sandy beaches, surrounded by dense rain forest. The Ogooué River is 75–100 m wide at Doumé, 3 m in depth, and the water had low conductivity (13.9 µs/cm) at pH 7.04 and 6.66 mg/L O_2 (83.1% saturated) at 26.7 °C. The Sébé River is 55–75 m wide, approximately 3.1 m deep, 16.0 µs conductivity, 7.08 pH and 7.5 mg/L O_2 (93.6% saturation) at 26.6°C).

Lateral head profile straight and downward sloping from a point half way between opercular opening and tip of the snout, slightly concave above the eye in some specimens. Head and snout 'V'-shaped when viewed dorsally (Figs 9D and 15), snout angle, 38–50° intermediate between that of *P. curvifrons* and *P. sphekodes* (Fig. 5D, G, Table 2). HL, 19.6–24.6% SL, similar to *P. sphekodes*, but shorter than *P. curvifrons* (Fig. 5A). HD measured from external landmarks 64.8–79.8% HL, or HL/HD = 1.13–1.35. When measured from radiographs, HLx/HDx = 1.25–1.38, non-overlapping with *P. sphekodes* (Fig. 4). HW 38.3–46.9% HL. In lateral view, snout tip lies along mid-horizontal line. Teeth bicuspid, 5 (rarely 4) in upper and 6 in lower jaws.

Mouth small, rictus directly beneath nares. Chin slightly swollen below gular region, not extending beyond snout. Eye small, ED 10.6–15.0% HL (Fig. 5F). Eye socket forms light ring around dark eyeball, with gold iris and dark centre. IOW 22.4–31.4% HL. Anterior naris at about 1/3 distance from snout tip to eye, slightly below line drawn through centre of eye, posterior naris halfway between anterior naris and eye, level with lower margin of eye. Opercular opening begins anterior to base of pectoral fin. POL 62.8–68.1% HL.

Pectoral-fin origin beneath posterior terminus of opercular opening, slightly below mid-horizontal line, pectoral length 14.6–16.8% SL, 10–12 rays. Pelvic-fin origin at 34.6–38.8% SL, length 8.2–11.1% SL, positioned ventrally, 6 rays. Pre-dorsal distance 61.4–66.1% SL; anterior margin of dorsal fin gently convex, trailing margin concave in first third, remainder levels off at 1/2 DFH. Maximum DFH 59.0–83.2% DFL, 19–21 total rays. Anal-fin origin slightly anterior to dorsal-fin origin: dorsal-fin origin above seventh anal ray (fifth branched ray).

Anal fin mirrors general shape of dorsal fin, maximum height 50.4–71.8% AFL. In males, anterior AFR thickened and stiff, noticeable notch in body spanning anterior half of anal-fin base. Anal-fin base terminus directly beneath that of dorsal fin, rays 24–26. Lobes of caudal fin rounded, equal, slightly wider than caudal peduncle, deeply cleft, scaled at the bases.

Scales fine, cycloid, absent from head. Pierced lateral line scales 57–72, 9–12 scale rows between anterior base of dorsal fin and lateral line, 10–14 scale rows from pelvic fin to lateral line. Circumpeduncular scales 12.

Vertebrae: 41–44 total, 18 pre-caudal and 22–26 caudal.

Figure 12. Holotype of ***P. ntotom*** **sp. nov**. CUMV 98138, tag number JPS-1189, male, 178 mm SL, from top to bottom photographed when alive, preserved in alcohol left and right sides, and radiograph. Scale bars = 1 cm.

Coloration. All fins with lightly to heavily pigmented rays, membranes hyaline. No dark band bases of dorsal and anal fins. Body darker dorsally, lighter ventrally. When alive, tan to light chocolate brown body with olive accents on top of head, back and belly. Mouth, chin and sometimes gular region unpigmented, white to grey. Many small white pores (mormyromast and ampullary electroreceptors) visible on top of head and back, with fewer, large white pores (Knollenorgans) on head. Preserved specimens are uniform greyish-brown.

Electric organ discharge. EOD composed of biphasic pulses, head positive then negative, total duration, 4.79 ± 1.1 ms (Fig. 14A, C; Table 3). Width, W1, of first peak 2.25 ± 0.429 ms, approximately equal to width of second peak (Table 3). Power spectrum peak, 265 ± 67 Hz. Other quantitative measures in Table 3 and Fig. 14. Marked inflection point on first rising phase of EOD in advance of peak P1; first derivative of EOD with two positive peaks before P1 (Fig. 14B, arrows 1 and 2), contrasting with *P. sphekodes*, which lacks an inflection point and has but a single peak in the first derivative (Fig. 8B). No head-negative peak in advance of P1 (see 20× expanded trace in Fig. 14A) as occurs in all mormyrids with Type Pa electrocytes (*P*enetrating stalks with *a*nterior innervation), indicating that electrocytes are type NPp (i.e. have *N*on-*P*enetrating stalks with *p*osterior innervation), the same as *P. sphekodes* (not shown).

The EODs of *P. ntotom* sp. nov. differ between males and females (Figs 2 and 14C) with a corresponding difference in EOD power spectrum (Figs 2 and 14E). EOD duration of males, significantly longer than that for females (Student's $t = 2.107$, $P < 0.05$, Table 3). Widths of the first and second peaks nearly equal in *P. ntotom* sp. nov. both for males and females (Table 3) contrasting with *P. sphekodes* where the first peak is longer than the second, especially for males. Variation in EOD duration amongst male *P. ntotom* sp. nov. results from EOD elongation during male sexual maturation – only appearing in the larger males during the breeding season. Adult males and females recorded during the dry season have similar EODs, a common pattern among mormyrids studied in the laboratory (Kirschbaum, 1984, 1987) and in the field (Bass *et al.*, 1983).

Distribution: *Paramormyrops ntotom* sp. nov. is found in Gabon in the Ogooué River and some of its tributaries (Fig. 10). We have confirmed its presence in the lower Ogooué near Lambaréné, the Okano River near Mitzig, the middle Ogooué near Lopé and the upper Ogooué from Doumé to Franceville. This species is notably missing from the Ivindo River, a major tributary of the Ogooué to the North East of Gabon, connected to the Ogooué through a series of major waterfalls.

Etymology: The species name, *ntotom* is the word for mormyrid fish in the language of the Fang people from northern Gabon, Equatorial Guinea and southern Cameroon.

KEY TO THE SPECIES OF *PARAMORMYROPS* FROM LOWER GUINEA

Combined with the summary figure (Fig. 16) this key can be used to distinguish among seven described and one undescribed species of *Paramormyrops* from Lower Guinea. *P. retrodorsalis* (Nichols & Grissom, 1917), *P. tavernei* (Poll, 1972) and *P. jacksoni* (Poll, 1967) are excluded here as they reside outside this region.

1. Teeth bicuspid, 7 in upper jaw, 8 in lower jaw……*P. hopkinsi*

   Teeth bicuspid, 5 in upper jaw, 6 in lower jaw……2

2. 16 or more scales around the caudal peduncle ……3

   12 scales around caudal peduncle…… ……5

3. Lower jaw profile straight, submental swelling reduced or absent……4

   Lower jaw profile concave, submental swelling present……*Paramormyrops batesii*

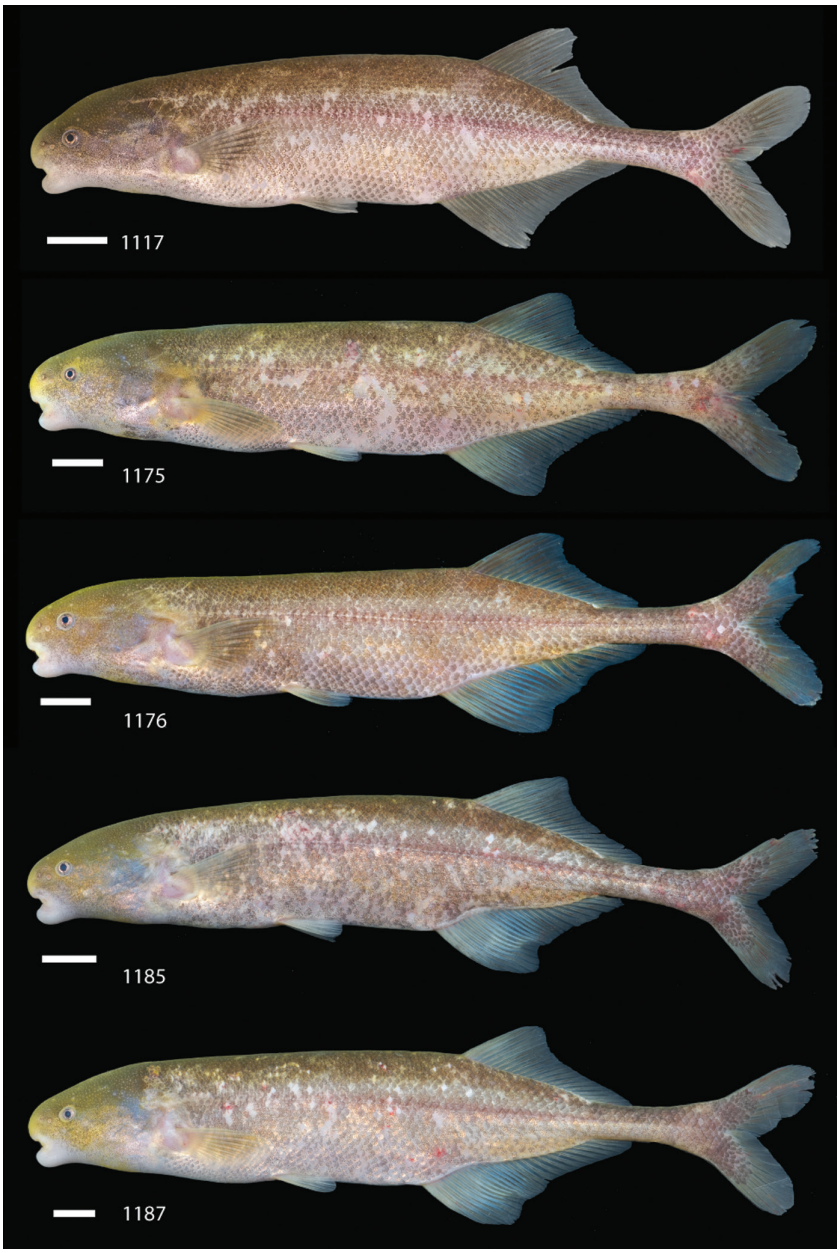

Figure 13. Variation in ***P. ntotom* sp. nov.** illustrated by five specimens from the Ogooué River: CUMV 96811 tag number JPS-1117, female, 117 mm; CUMV 98091 tag number JPS-1175, male 130 mm SL; CUMV 98092 tag number JPS-1176, male, 154 mm SL; CUMV 98134 tag number JPS-1185, male, 176 mm and CUMV 98136 tag number JPS-1187, male 165 mm.

4. Pre-dorsal distance 58–62% SL; CPL 20.7–25.5% SL……..*P.* sp. *OFF*

   PDD 55.3–59.4% SL; CPL 24.2–29.8% SL……*P. longicaudatus*

5. Head profile blunt or U shaped when viewed from above……6

   Head profile sharp or V shaped when viewed from above……7

6. Forehead slightly concave viewed from side; HL 24.9–27.6% SL; caudal peduncle slender, its depth 3.7–4.7% SL; interorbital distance 110–133% SNL……*P. gabonensis*

   Forehead rounded: HL 19.5–28% SL; caudal peduncle depth 4.1–7.5% SL; interorbital distance 121–202% SNL……*P. kingsleyae*

7. Upper profile of head downward sloping, slightly concave: mouth subterminal: Pre-pectoral

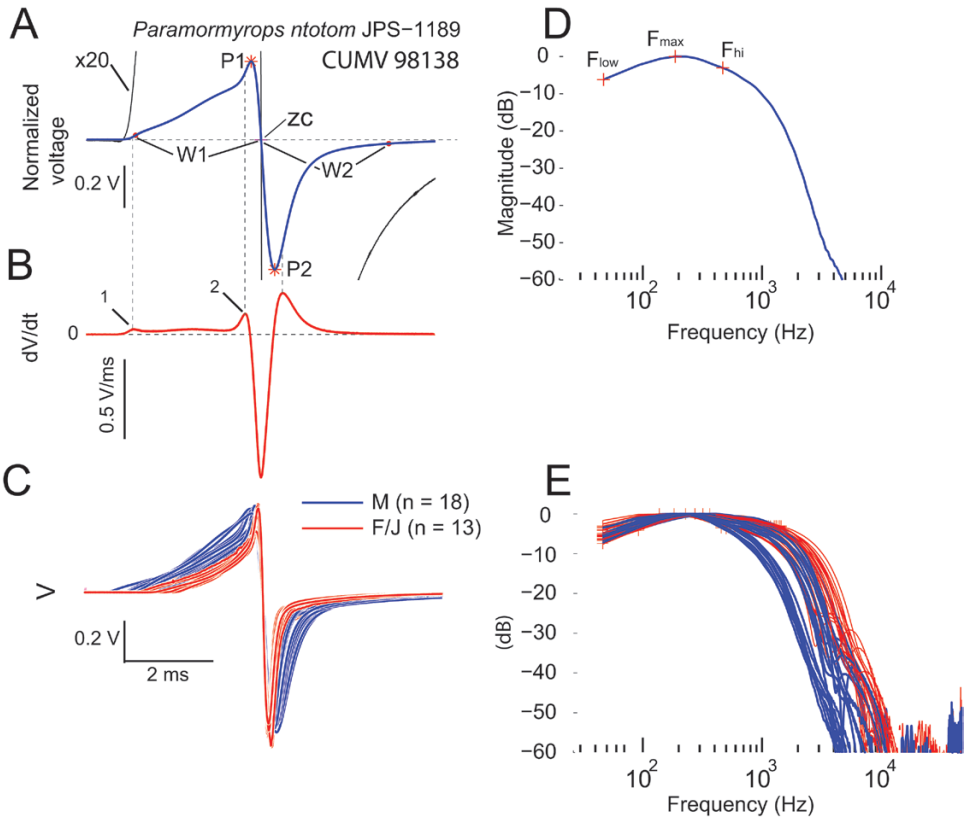

Figure 14. Electric organ discharges (EODs) from ***P. ntotom* sp. nov.** EOD waveforms plot voltage versus time. Voltage is normalized by setting the peak-to-peak voltage to 1.0 V. The time base is in (C). (A) EOD of holotype, CUMV 98138 tag number JPS-1189, male, SL 178 mm. The first peak, P1, is head-positive and the second, P2, is head-negative. Overall duration is 5.813 ms, measured between the two red dots. The 20× expanded trace (black) indicates the absence of a head-negative phase preceding P1. Abbreviations are as in Figure 10. (B) Time derivative of EOD shown in (A), indicating two points where dV/dt goes through a local maximum leading to inflection points in the EOD (dashed lines). (C) Superimposed EODs from 18 males (blue) and 13 females and juveniles (red) show a clear sex difference in EOD duration. (D) Power spectrum of the EOD of holotype, with magnitude measured in dB relative to the peak power plotted against frequency in Hz. Frequency at peak power indicated by $F_{max.}$ The frequencies where the magnitude of the power spectrum drops 3 dB below the peak power are indicated by F_{low} and F_{hi}. (E) Superimposed power spectra of traces shown in (C) demonstrate that spectral power emphasizes higher frequencies among females compared to males, as expected.

distance large, PPCD more than 37% SL .....*P. curvifrons*

Upper profile of head gently downward sloping or rounded, mouth terminal; pre-pectoral distance small, PPCD less than 37% SL.....8

8. IOW/SNL > 1.0; CPD/CPL < 0.29; HLx/HDx 1.25 or more; EOD duration > 3 ms.....***P. ntotom* sp. nov.**

IOW/SNL < 1.04; CPD/CPL > 0.28; HLx/HLx < 1.24; EOD duration < 1.5 ms.....
.....*P. sphekodes*

DISCUSSION

The identity of *P. sphekodes* has been confused for more than a century. At the time of its description and for long afterwards it was not understood that *P. sphekodes* was one member of a species flock (Sullivan *et al.*, 2002) among which interspecific morphological differences are subtle (Arnegard *et al.*, 2010a). As the first of this group to have been described, its name was widely applied to specimens not only from other parts of the Ogooué basin (Günther, 1896), but also from neighbouring river basins in southern Cameroon (Boulenger, 1909; Kamdem Toham, 1998), Equatorial Guinea (Román, 1971) and Congo (Gosse, 1984). These identifications – all of which should be re-examined

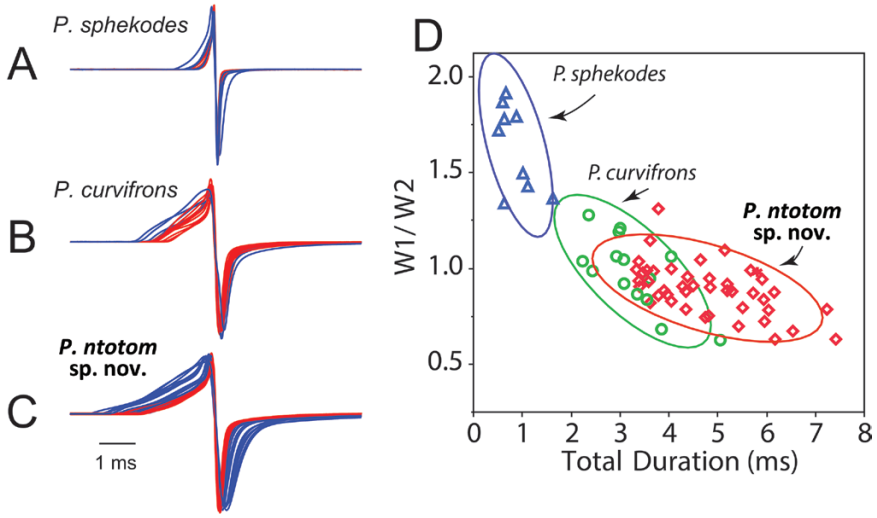

Figure 15. EODs from (A) *P. sphekodes* from the Ogooué River, (B) *P. curvifrons* from the Ivindo River and (C) ***P. ntotom* sp. nov.** from the Ogooué River. Each is plotted on the same time scale, all with head positivity upwards. (D) Scatter plot of EOD duration versus the ratio W1/W2 – the widths of the first and second phases of the EOD illustrated in Figs 10 and 14. EOD total duration and W1/W2 overlap for the allopatric pair, *P. curvifrons* and ***P. ntotom* sp. nov.**, but not for the sympatric pair, *P. sphekodes* and ***P. ntotom* sp. nov.**

– were reflected in the distribution map of this species published in Hopkins *et al.* (2007).

Here we have clarified the identity of this species by presenting evidence for a good match between the lectotype and paralectotype of *P. sphekodes* and nine recently collected specimens from Doumé, the type locality on the Ogooué River and from a site on the Sébé River, 45 km distant. Our own focused collecting of mormyrids in 1993, 1994, 1998, 1999, 2001, 2002, 2006 and 2009 at localities both farther up the Ogooué near Franceville and below at Lopé and Lambaréné, as well as in multiple other parts of the basin (e.g. the Ivindo, Okano and Ngouné River tributaries) and in neighbouring basins (Ntem, Woleu, Nyanga and Congo) failed to produce a single specimen of this species. After review of our collections at the CUMV as well as CAS, MNHN and MRAC, we remain unaware of other specimens of *P. sphekodes* among the specimens in these collections apart from the two types and the nine new specimens. Some of the specimens currently identified as *P. sphekodes* in museums may belong to *P. ntotom* sp. nov. or to yet undescribed species in this genus.

While the actual distribution of *P. sphekodes* obviously extends beyond the two sites from which we know it, we tentatively conclude that it is a narrowly distributed species, endemic to a relatively small part of the upper Ogooué basin. Its preferred habitat in shallow rapids may be a factor in its rarity in our collections. By contrast, the new species we describe here, *P. ntotom* sp. nov., with which *P. sphekodes* can easily be confused, is common in the upper, middle and lower Ogooué River channel and has also been collected in the Okano River near Mitzic.

Until now, uncertainty as to which *Paramormyrops* specimens with sharp snouts and NPp-type electric organs from our recent collections were *P. sphekodes* had forestalled description of new species. Before collection of the 'short-headed' species from Doumé, we had regarded the species we earlier called 'SN4' (Sullivan *et al.*, 2002, 2004), here described as *P. ntotom* sp. nov., as the best candidate for *P. sphekodes*. As it turns out, *P. sphekodes* had been entirely unknown to us. Without our new collections from the type locality of Doumé – surprisingly the first since Marche in 1876–1877 (Cutler, Apse, Cavelier *et al.*, 2016) – we could not have successfully resolved this taxonomic problem.

In addition to morphological comparison, collection of electric signals and DNA data from these specimens proved essential. Had we not observed the different EOD waveforms of *P. sphekodes* and *P. ntotom* sp. nov., we would probably have overlooked the slight difference in head proportions between them. Recording EODs when collecting mormyrids should ideally be standard practice as it is relatively easy to do with consumer electronics (see Material and Methods and Sullivan, 2016). A library of vouchered mormyrid EOD recordings being assembled at the Macaulay Library of the Cornell Laboratory of Ornithology will facilitate comparison of EODs of newly collected fishes with identified specimens.

Mitochondrial phylogenies are imperfect estimators of species relationships in this genus likely due to incomplete lineage sorting and introgression of the

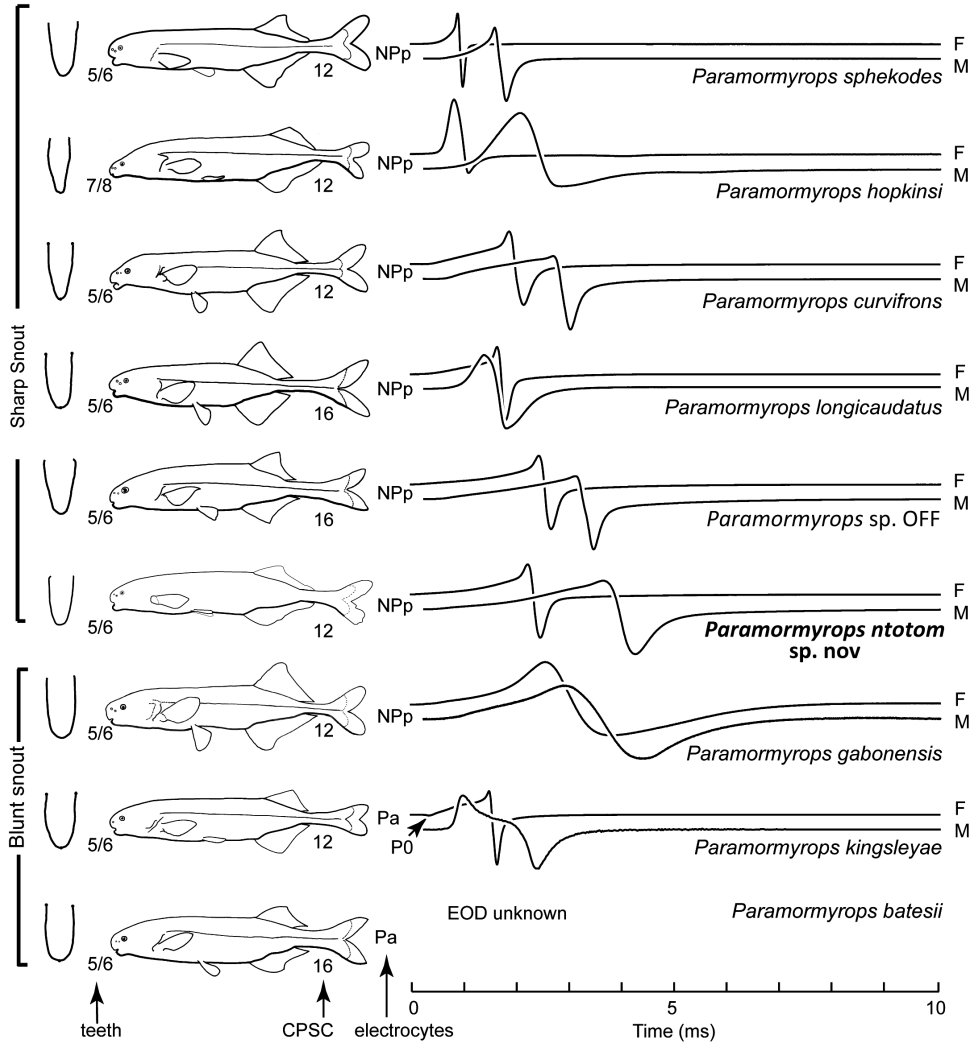

Figure 16. Nine species of *Paramormyrops* from Lower Guinea showing, from left to right, head shape viewed from above, the outline of the body, and representative female and male EOD waveforms. Head shapes are *camera lucida* tracings of the holotypes for each species from the snout to end of opercular opening. The first six have sharp V-shaped head profiles and the last three have relatively blunt U-shaped heads. All but the last two have electric organs composed of Type NPp electrocytes (exhibiting *N*on-*P*enetrating stalks innervated on the *p*osterior face). The last two have electric organs composed of Type Pa electrocytes (with *P*enetrating stalks innervated on the *a*nterior face). All known mormyrids with Type Pa electrocytes have an initial, head-negative peak, P0, in the EOD waveform as illustrated here for *P. kingsleyae*. The P0 peak is absent in all species with Type NPp electrocytes. The EOD of *P. batesii* is unknown, but the electric organ is composed of Type Pa electrocytes.

mt genome across species boundaries (Sullivan *et al.*, 2002, 2004). Nevertheless, the lack of shared haplotypes among individuals of the two forms was an important third line of evidence for their heterospecificity. Combined study of morphology, electric signals and DNA provides a powerful framework in which to identify and describe new mormyrid species, as a number of other recent works on mormyrid taxonomy have shown (see Kramer & Swartz, 2010; Lavoué *et al.*, 2010, 2014; Sullivan *et al.*, 2016).

Previously, Sullivan *et al.* (2004) recognized a 'curvifrons complex' within the phylogenetic tree of *Paramormyrops* constructed from analysis of AFLP data (amplified fragment length polymorphisms). This multilocus dataset was much more successful at recovering monophylyetic groups consistent with morphospecies than were mitochondrial phylogenies. The 'curvifrons complex' included *P. curvifrons* and *P. longicaudatus* from the Ivindo River of Gabon, *P. ntotom* sp. nov. described here (coded as 'SN4' and as

'IN1' 1844 in Sullivan (2004) Fig. 2, from the mid to lower-Ogooué, coded as 'SN4' from the upper Ogooué, and as *B.* cf. *curvifrons* #4149 from the Okano River), plus six additional undescribed taxa coded as SN2, NGO, SN3, OKA, BN2, SN7 and OFF. All of these taxa have electric organs with Type NPp electrocytes, and simple biphasic EODs, and all have sharp snouts that are V-shaped when viewed dorsally except for 'BN2'. We expect that *P. sphekodes* also belongs to the 'curvifrons complex' That this group was not recovered as a clade on the cyt-*b* tree presented in Fig. 6 is consistent with the findings of Sullivan *et al.* (2004). Better resolution of the species tree for *Paramormyrops* and the placement of *P. sphekodes* would be best addressed via a newer technique employing high-throughput sequencing.

Resolving the identity of *P. sphekodes* – redescribing it and describing its cryptic, widespread close relative as we have done here – is an important first step in the systematic treatment of this remarkable *Paramormyrops* species flock of the Ogooué and neighbouring river basins of West-Central Africa.

Additional material examined

Paramormyrops curvifrons: Holotype: Ivindo River, by M'Passa, Makokou: MRAC 75-24-P-132, 107.35 mm SL, A. Heymer, 4 November 1974.

Non-type specimens: **Ivindo River, 2–3 km downriver of Makokou, 0.5 km upriver of the Loa-Loa rapids**: (0.517, 12.833): CUMV 75449 (5, specimen nos. 1036, 1039, 1042, 1043, 1045) 91.86–118.65 mm SL, C.D. Hopkins and M.A. Friedman, 31 October 1993. (0.525, 12.783): CUMV 75411 (1, specimen no. 1395) 118.04 mm SL, C.D. Hopkins and G.D. Harned, 12 September 2014. (0.550, 12.850): CUMV 75408 (1, specimen no. 1426) 98.15 mm SL, C.D. Hopkins, 15 September 1994. (0.550, 12.850): CUMV 75409 (6, specimen nos. 1434, 1440, 1441, 1442, 1443, 1444) 101.01–123.76 mm SL, C.D. Hopkins, 16 September 1994. (0.5, 12.81667) CUMV 75410 (7, specimen nos. 1446, 1447, 1448, 1449, 1450, 1451, 1452) 76.91–113.04 mm SL, C.D. Hopkins and G.D. Harned, 18 September 1994. (0.517, 12.783): CUMV 75407 (1, specimen no. loc cdh 94–42B#4) 127.03 mm SL, C.D. Hopkins *et al.*, 9 September 1994.

EOD recordings: **Loa-Loa rapids, Ivindo River below Makokou** (0.522, 12.825): JP Sullivan *et al.*, 10 May 2011: CUMV 96847 (13, specimen nos. JPS-1003, JPS-1006, JPS-1007, JPS-1009, JPS-1017, JPS-1018, JPS-1021, JPS-1023, JPS-1027, JPS-1031, JPS-1041, JPS-1049, JPS-1066) EOD nos. 197350–197362.

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