

Bioelectric Fields of the African Marbled Lungfish *Protopterus aethiopicus* (Sarcopterygii: Protopteridae), African (*Heterotis niloticus*) and South American Silver (*Osteoglossum bicirrhosum*) Arowanas (Actinopterygii: Osteoglossidae): Primitive Electrogenesis?¹

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Abstract—Sporadic weak electric discharges were recorded from the African marbled lungfish (*Protopterus aethiopicus*), African arowana (*Heterotis niloticus*) and South American silver arowana (*Osteoglossum bicirrhosum*). In all species, the discharges were registered from a pair of freely swimming individuals left for several hours in an experimental tank, or evoked by tactile stimulation in the lungfish and the African arowana. Maximum amplitudes of recorded pulses ranging from 1.5 mV in *Osteoglossum* to 10 mV in *Protopterus* and *Heterotis*, as well as the coordinated discharge patterns, allow us to suggest the existence of anatomically and physiologically specialized electrogenic tissue in these species. The phylogenetic and evolutionary significance of primitive electrogenesis in the lobe-finned and bony-tongue fishes is discussed.

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INTRODUCTION

Electroreception is found in many primitive groups of primarily aquatic vertebrates including lampreys, cartilaginous fishes, lobe-finned fishes and in two primitive orders of ray-finned fishes (polypteriforms and acipenseriforms) as well as in few lineages of teleostean fishes (Osteoglossomorpha, xenomystins and mormyriiforms; Ostariophysi, siluriforms and gymnotiforms). Moreover, electroreception could be surmised in many extinct fish groups (Hopkins, 2009). In contrast to electroreception, electrogenesis is not considered an ancestral vertebrate feature (Northcutt, 1986; Zupanc and Bullock, 2005). According to Albert and Crampton (2006), among fishes the capacity to produce regular coordinated electric discharges has evolved independently in at least 11 lineages.

Finding of electrogenesis in bichirs (*Polypterus delhezi* and *P. senegalus*) (Baron and Pavlov, 2003) and some catfishes representing four families Mochokidae (Hagedorn et al., 1990; Baron et al., 1994a, 2002; Boyle et al., 2014), Clariidae (Baron et al., 1994b, 2008; Olshansky et al., 2002), Claroteidae (Baron et al., 1996a,b; Orlov et al., 2015), Siluridae (Morshnev and Olshansky, 1997; Baron and Olshansky, 2009)

leaves open the possibility that there are more sporadically discharging weakly electric fish to be discovered in various taxa traditionally viewed as electrically “silent” (Zupanc and Bullock, 2005). The more so, there are many electroreceptive fishes considered yet as electrically “silent”. It is also reasonable to suggest that the ancestors of highly specialized continuously discharging electric fishes (the gymnotiforms and mormyriiforms) exhibited a primitive stage in the evolution of electric organs similar to those found in bichirs and catfishes (Zupanc and Bullock, 2005).

Present communication describes the electric discharges recorded from the marbled lungfish *Protopterus aethiopicus* Heckel, a representative of the lobe-finned fishes, and the African arowana, *Heterotis niloticus* (Cuvier), a representative of the bony-tongue fishes, the primitive lineage of teleostean fishes. Recording of the electric activities in the lungfish and African arowana was conducted in the field using individuals from natural populations. We also report the electric activity of individuals of the South American silver arowana *Osteoglossum bicirrhosum* (Cuvier) obtained through the aquarium trade. Phylogenetic and evolutionary applications of these findings are discussed.

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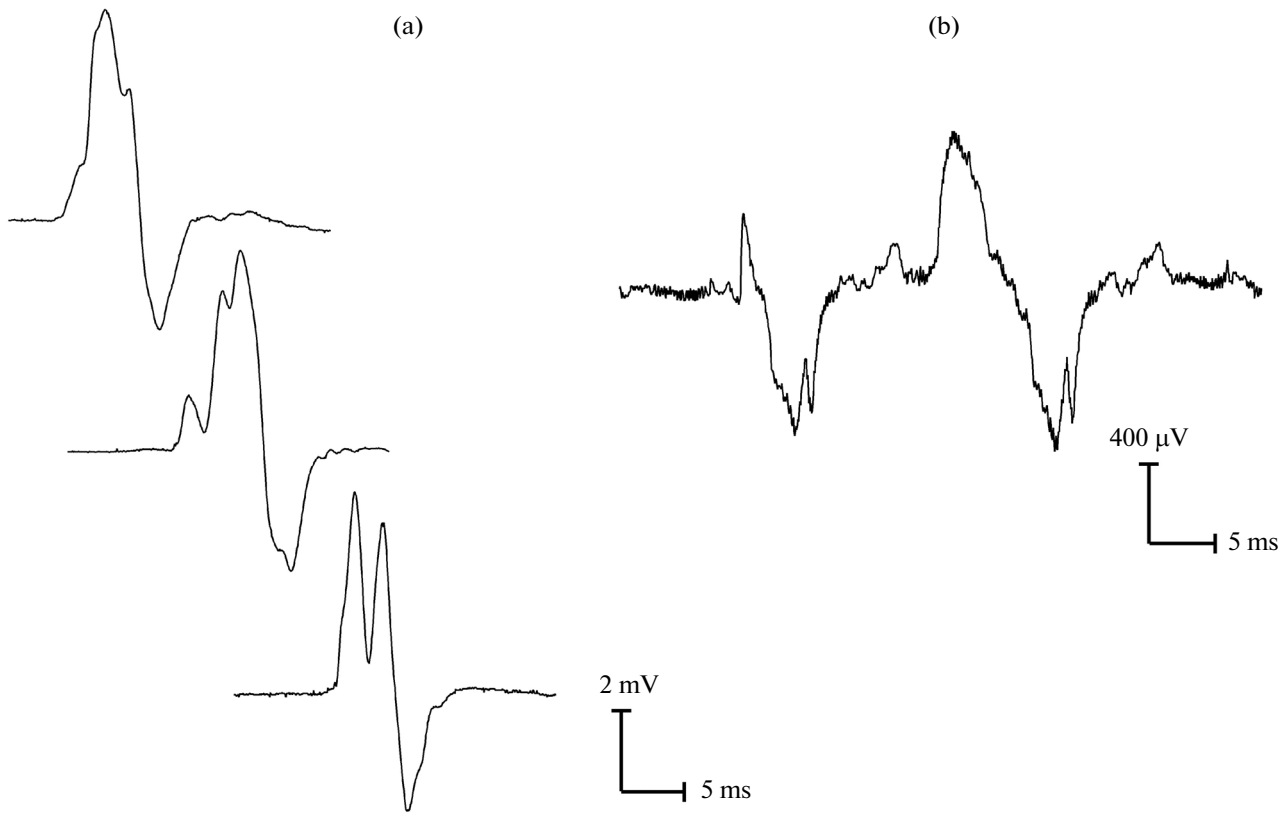


Fig. 1. Electric discharges of *Protopterus aethiopicus*: (a) from half-grown and adult individuals (298–524 mm *TL*), discharges evoked by the tactile stimulation, their traces scaled to the maximum peak-to-peak amplitude; (b) spontaneous pulses recorded from a pair of juveniles (62–72 mm *TL*).

MATERIALS AND METHODS

Five individuals of *Protopterus aethiopicus* (62, 72, 298, 371 and 524 mm in total length, *TL*) and three individuals of *Heterotis niloticus* (162, 234 and 282 mm in standard length, *SL*) were obtained from the White Nile drainage in western Ethiopia, an additional individual of the latter species (267 mm *SL*) was obtained from the Blue Nile drainage in western Ethiopia. Within a few hours after capture fish were delivered in plastic containers with aerated water to a field laboratory, where they were maintained in 80-liter plastic drums with oxygenated and filtered water from the place of their origin. Within 2–48 hours after fish were obtained, recordings were taken from an individual or a pair of individuals placed in the plastic experimental tanks of various dimensions dependent on fish size (40 cm long by 10 cm wide by 20 cm high or 60 cm long by 40 cm wide by 40 cm high or 100 cm long by 40 cm wide by 60 cm high) filled with water from the river. Recordings were taken not earlier than in half an hour after placement fish in the experimental tank. Water temperature and conductivity during recordings ranged from 23.5 to 29°C and from 96 to 236 μS/cm. Two individuals of *Osteoglossum bicirrhosum* (approximately 15 cm *SL*) were obtained from aquarium dealers (Aqua Logo, Moscow). Water temperature and

conductivity during recordings were 27.0°C and 522 μS/cm, respectively.

Each recording session was started with registration in the empty experimental tank to be sure that our recordings would not be spoiled by external interference. Recordings were taken from freely swimming fish with previously described methods (Baron et al., 2002, 2008; Baron and Pavlov, 2003) with two electrodes (stainless steel plates 6 by 6 cm) attached vertically to the opposite walls of experimental tank. Signals were amplified 100x with a differential preamplifier (Grass P15), band-pass-filtered from 0.1 Hz to 10 KHz and digitized at 200 KHz (12-bit A/D converter) with the Multifunction Data Acquisition (DAQ) device (DAQ-card AI-16E-4, National Instruments) connected to a PC, where EODs were stored and visualized by means of custom-made software developed with the use of LabView v. 7.0.

RESULTS

Pulses recorded from *Protopterus aethiopicus* were biphasic with an initial head-positive phase followed by a weaker head-negative phase (Fig. 1a). Duration of the first and second phases was typically 6–8 and 2–3 ms, respectively. The presence of multiple peaks in

most discharges probably is a result of summation of shorter pulses that are not perfectly synchronous. Similar summation was suggested based on comparison of the two types of electric discharges in the catfish *Auchenoglanis occidentalis* (Orlov et al., 2015). All pulses recorded from the three larger *Protopterus* individuals (298–524 mm *TL*) were provoked by tactile stimulation (touching the dorsal surface of the fish with a glass rod). Fish were stimulated and discharges recorded when they stayed in the center of the experimental tank with their body in line with the recording electrodes. No spontaneous discharges were recorded from the larger individuals.

Only two almost simultaneous spontaneous pulses were recorded from a pair of juvenile *Protopterus* (62–72 mm *TL*) placed together in the experimental tank for 11 hours (Fig. 1b). Albeit the polarity of discharge phases of juvenile pulses could not be determined, the waveform of their spontaneous discharges resembled those obtained by stimulation from the larger individuals. Peak-to-peak amplitude of the juvenile discharges was apparently lower than the maximum recorded amplitude in the larger individuals (1.5 versus 5–8 mV) despite the different recording conditions, i.e. using the smallest experimental tank for juveniles.

All pulses recorded from the African arowana *Heterotis niloticus* appeared to be the tetra-phasic discharges with the initial head-negative phase characterized by the largest relative amplitude and subsequent two head-positive and one head-negative phases characterized by a gradually decreasing relative amplitudes (Figs. 2a and 2b). All four phases were approximately equal in duration (1–2.5 ms), while the amplitude ratio for the 2nd, 3rd and 4th phases differed slightly among individuals (Figs. 2a and 2b). Discharges could be provoked by tactile stimulation (Fig. 1b), but spontaneous discharges were also recorded from the three individuals left in pairs in the experimental tank for long periods of time. During ten hours of registration 15 discharges were recorded from the most active pair, four of them are presented in Fig. 1a. Despite the similarity of the waveform of these discharges, it is not clear, whether one or both individuals emitted them.

All discharges recorded from the silver arowana *Osteoglossum bicirrhosum* (Fig. 1c) were similar to those of *Heterotis niloticus* (Figs. 2a and 2b), but their waveform was less stable. Maximum peak-to-peak amplitude was around 1.5 mV. Polarity of phases was not determined because only five spontaneous discharges were recorded from a pair of individuals left for 19.5 hours in the experimental tank. The discharge amplitudes recorded from freely swimming fish with unknown position in relation to electrodes are estimates for provisional comparisons only. Nevertheless, the difference of maximum amplitudes reported for the two arowanas could be explained by the higher water conductivity in the case of *Osteoglossum*.

DISCUSSION

Among five recently discovered groups of the sporadically discharging weakly electric fishes (bichirs and four catfish families), the electric organ is anatomically identified only in the catfish genus *Synodontis* (Hagedorn et al., 1990; Boyle et al., 2014). Localization of the electric command nucleus in the medulla oblongata is provisionally demonstrated for the *Synodontis* and *Clarias* (Baron et al., 2002). At the early stages of the electric organ evolution, the electrogenic capacity is developing most probably via synchronization of action potentials from some peculiar muscle fibers (Bullock, 1999), as it was shown for electrogenic activity of the sonic muscles in *Synodontis*. Along with morphological and physiological transformations of the evolving electrogenic tissues (in cell form and alignment, functional asymmetry of cell membrane, etc.), they required improved neural coordination mechanism (Bennett, 1971).

Despite the lack of histological and anatomical data of electrogenic tissue in the lungfish and arowanas, we postulate nevertheless the existence of anatomically and physiologically specialized electrogenic tissue, i.e. a primitive electric organ, in these fish for the following reasons. The species studied apparently produce rare but repetitive coordinated electric discharges with a maximum amplitude of 1–2 mV in *Osteoglossum* and up to 10 mV in *Protopterus* and *Heterotis* (under the present recording conditions), compared to amplitudes of myograms in fish not exceeding a hundred of microvolts (Barham et al., 1969; Basov, 1985). Discharges of the fish studied could be considered as coordinated because of reproducibility of the discharge waveform within the species. The discharge coordination seems to be substantially higher in arowanas compared to lungfish. We have to emphasize the similarity of discharge waveforms in the two arowanas though the polarity of the discharge phases was not determined in the silver arowana (*Osteoglossum bicirrhosum*). The coordinated weak electric discharges in the Asian arowana *Scleropages* sp., however, differ from those typical of *Heterotis* and *Osteoglossum* with maximum amplitudes for *Scleropages* not exceeding 150 μ V (Olshansky, 2014).

Until now, the dominating view was that the electrogenesis in the sporadically discharging weakly electric catfishes (Mochokidae, Clariidae, Claroteidae and Siluridae) and electric catfishes (Malapteruridae) has evolved independently (Alves-Gomes, 2001; Albert and Crampton, 2006; Boyle et al., 2014). There are, however, morphologic (Pinna, de, 1993) and molecular (Sullivan et al., 2006) data showing close phylogenetic relationships between at least three of these catfish lineages (Claroteidae, Mochokidae and Malapteruridae). This raises a question about the presence of an electric organ in the common ancestor of these catfish groups. Finding of electrogenesis in some catfish lineages is of particular interest because of the

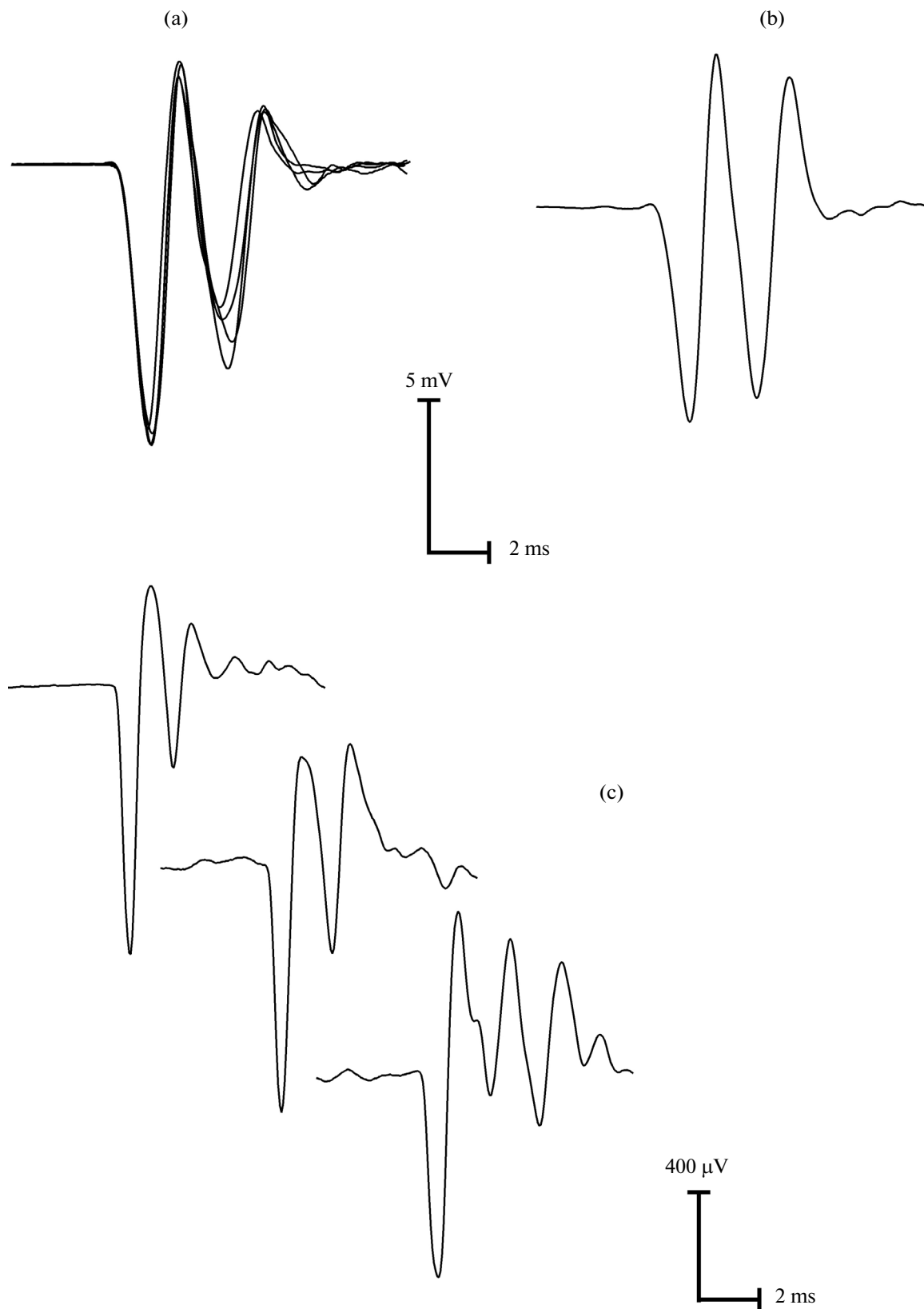


Fig. 2. Electric discharges of arowanas: (a) superimposed traces of four spontaneous pulses recorded from a pair of the African arowanas *Heterotis niloticus*; (b) a pulse evoked by the tactile stimulation from an individual of the same species; (c) spontaneous pulses recorded from a pair of the silver arowanas *Osteoglossum bicirrhosum*. Discharge traces were scaled to the maximum peak-to-peak amplitude in each species.

close phylogenetic relationships between the siluriforms and gymnotiforms with their highly specialized electrogenic and electroreceptive systems. Even if in contrast to the previously accepted opinion (Fink and Fink, 1981, 1997; Alves-Gomes, 1999) these two orders are not sister groups, the hypothesis about origin of the ampullary-type electroreception in their common ancestor may be valid (Lavoué et al., 2012; Chen et al., 2013). We believe that the hypothesis concerning an electrogenic ancestor of these two groups deserves consideration, especially if electrogenesis will be found in other phylogenetically distant catfish lineages.

Previously, the highly specialized electrogenic system of mormyriiforms seemed to be isolated phylogenetically, while the ampullary-type electroreception is found in the two African genera (*Papyrocranus* and *Xenomystus*) of Notopteridae, a sister group of the mormyriiforms (Bradford, 1982; Bullock and Northcutt, 1982; Lavoué and Sullivan, 2004). Four genera *Osteoglossum*, *Scleropages*, *Heterotis*, and *Arapaima* belong to the family Osteoglossidae, a sister group of notopterids and mormyriiforms (Lavoué and Sullivan, 2004; Inoue et al., 2009). The present finding of electrogenesis in the osteoglossids indicates the possibility of an early origin of electrogenic capability in the evolution of the bony-tongue fishes (Osteoglossomorpha). The puzzle is that electroreception is not found in all the osteoglossids, as well as in the two Asian genera of notopterids (*Chilata* and *Notopterus*), while all electrogenic fishes except stargazers (Uranoscopidae) are electroreceptive (Zupanc and Bullock, 2005). We wish to stress that the conclusion about the absence of electroreception in osteoglossids is based on the brain anatomy in only one species, *Osteoglossum bicirrhosum* (Bullock and Northcutt, 1982; Bullock et al., 1983). It has no electrosensory lateral line lobe (ELLL) in the octavolateral area of medulla, which is considered as an anatomic specialization obligatory associated with electroreception in Teleostei (Bullock et al., 1983). Neither anatomical data on brain structure in *Scleropages*, *Heterotis* and *Arapaima*, nor electrophysiological data on electroreception for any osteoglossid genera are published. The lack of electroreception is also demonstrated both anatomically and physiologically for *Pantodon* (family Pantodontidae), a sister group of Mormyriiformes plus Notopteridae plus Osteoglossidae, while for *Hiodon* (family Hiodontidae), a sister group of all other Osteoglossomorpha, only anatomical evidence for the lack of electroreceptive specialization of the brain has been reported (Bullock et al., 1983). Taking into account the present finding of the primitive electrogenesis in several osteoglossids, additional proof of non-electroreceptivity of this group, as well as looking for weak sporadic discharges in the African notopterids (*Papyrocranus* and *Xenomystus*) seem to be reasonable.

In contrast to arowanas, all three extant genera of the lungfishes are recognized as electroreptive: *Lepi-*

dosiren based on both anatomic and electrophysiological data, *Neoceratodus* and *Protopterus* based only on anatomical data (Bullock et al., 1983). Our data admit a communicative function of the weak electric discharges in *Protopterus*. The discovery of electrogenesis in the African lungfish, along with earlier reports of sporadic weak electric discharges in some catfishes and bichirs, extend the list of electroreceptive fishes possessing a primitive electrogenic system. Further findings of such groups seem to be probable. In general, the presence of electrogenesis in basal groups of various fish phylogenetic lineages coupled with indications of the presence of electric organs in some extinct agnathas (Stensio, 1927; Moy-Thomas and Miles, 1971) may raise a question about reappraisal of electrogenesis as an ancestral feature in the evolution of primarily aquatic vertebrates.

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