

## Article Addendum

# Magic trait electric organ discharge (EOD)

## Dual function of electric signals promotes speciation in African weakly electric fish

Philine G.D. Feulner,<sup>1,2,\*</sup> Martin Plath,<sup>3</sup> Jacob Engelmann,<sup>4</sup> Frank Kirschbaum<sup>5,6</sup> and Ralph Tiedemann<sup>1</sup>

<sup>1</sup>Institute of Biochemistry and Biology; University of Potsdam; Potsdam, Germany; <sup>2</sup>Department of Animal and Plant Sciences; University of Sheffield; Sheffield, UK; <sup>3</sup>Department of Ecology and Evolution; Institute of Ecology, Evolution and Diversity; J.W. Goethe-University of Frankfurt; Frankfurt, Germany; <sup>4</sup>Institute of Zoology; University of Bonn; Bonn, Germany; <sup>5</sup>Institute of Animal Sciences; Humboldt-University-Berlin; Berlin, Germany; <sup>6</sup>Leibniz-Institute of Freshwater Ecology and Inland Fisheries; Berlin, Germany

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A unique evolutionary specialization of African weakly electric fish (Mormyridae) is their ability to produce and perceive electric signals. Mormyrids use their electric organ discharge (EOD) for electrolocation and electrocommunication. Here we discuss the adaptive significance of the EOD in foraging (electric prey detection) in light of recent results demonstrating that mormyrid fish mate assortatively according to EOD waveform characteristics (electric mate choice). Therefore the EOD as a single trait pleiotropically combines natural divergent selection and reproductive isolation. Consequently we postulate the EOD as a “magic trait” promoting the diversification of African weakly electric fish.

Novel evolutionary specializations are thought to be one of the major driving forces of diversification.<sup>1,2</sup> Within African weakly electric fish (Mormyridae) the evolution of the electric organ discharge (EOD) may represent a key innovation promoting the radiation in this group of fish. Supporting evidence for the importance of the EOD for diversification has been identified in two well-studied mormyrid species flocks exhibiting a high degree of interspecific EOD variation: the Paramormyrops species flock from Gabon<sup>3-5</sup> and the Campylomormyrus species flock from the lower Congo River<sup>6-8</sup> (Fig. 1). These fish use their ability to produce and perceive electric signals to sense objects (active electrolocation<sup>9,10</sup>) and in a social context for electrocommunication.<sup>11,12</sup> In this paper we scrutinize support for the idea that divergent EOD types evolved to allow different ecotypes to exploit dissimilar food sources (leading to trophic niche segregation), and that EOD simultaneously also plays an important role

for conspecific mate attraction. Hence, EOD may be an example of a “magic trait”,<sup>13</sup> which is a trait shaped by disruptive natural selection but pleiotropically also affects pre-zygotic reproductive isolation, facilitating rapid speciation in African weakly electric fish.

### Electric Prey Detection

Besides their ability to produce electric signals, mormyrid fish are well known for their remarkable diversity in viscerocranial morphology (Fig. 2). Campylomormyrus species possess a trunk-like snout with a terminal opening and feed on insect larvae hidden in the sediment.<sup>14</sup> Within the sympatric Campylomormyrus species from the lower Congo River the shape of the rostrum shows the strongest degree of divergence in a morphometric analysis.<sup>6</sup> This points towards a role for disruptive natural selection driving ecological differentiation between closely related species, leading to trophic niche segregation.

A behavioral study highlighted the importance of active electrolocation for prey detection especially in the dark.<sup>15</sup> Mormyrids are nocturnal and often occur in turbid rivers, so the electric sense of these fish is likely to play a crucial role during food detection. As electrolocation is a frequency dependent process, the duration of the EOD affects the kind of prey items that can be detected best.<sup>16</sup> Mormyrid species with higher frequency components in their EODs, i.e., short duration EODs, should thus be able to detect smaller prey items. Indeed, sister species like *C. compressirostris* and *C. rhynchophorus*, which show marked differences in their EOD duration also show pronounced differences in their snout morphology, indicating the exploitation of different prey spectra. A recent study on the molecular evolution of sodium channel genes potentially shaping the electric signal, found support for positive selection acting on Na<sub>v</sub>1.4a within lineages of electric fish.<sup>17</sup> This gene lost its expression in the muscle tissue of electric fish and is solely expressed in the electric organ.

Interestingly, our recent study on Campylomormyrus<sup>18</sup> did not find any differences between the sexes in EOD even when only mature, reproducing specimens were considered. This finding is compatible with the idea that ecological adaptation rather than sexual selection drives divergence in EOD. However, our results

\*Correspondence to: Philine Feulner; Department of Animal and Plant Sciences; University of Sheffield; Sheffield S10 2TN, UK; Tel.: +44.114.2220112; Fax: +44.114.2220002; Email: P.Feulner@sheffield.ac.uk

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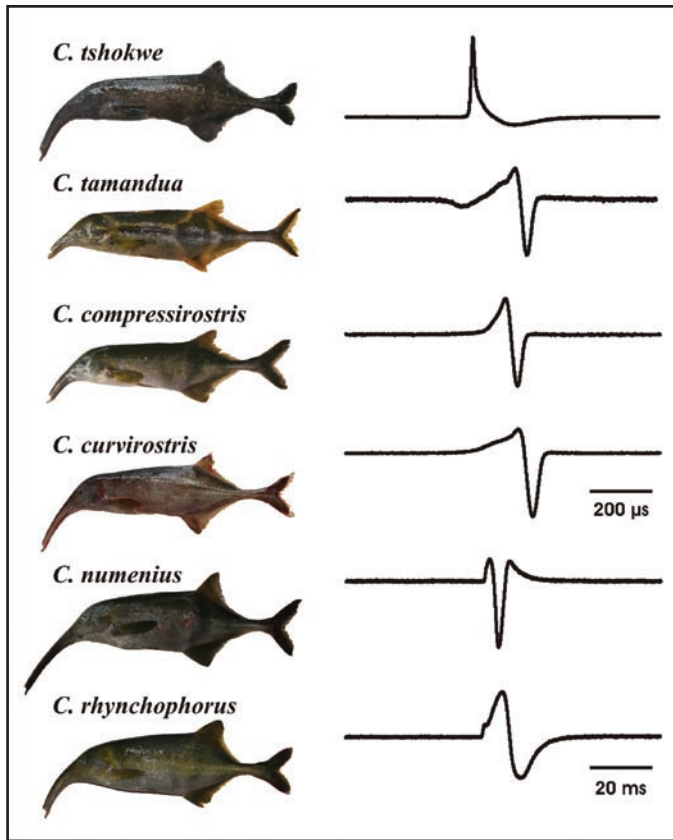


Figure 1. Interspecific variation in *Campylomormyrus* species of the lower Congo River. Morphological differentiation as demonstrated in the images is pronounced in the trunk-like elongated snout, the corresponding EOD vary largely in their waveform but also dramatically in the duration (note different scales indicated).

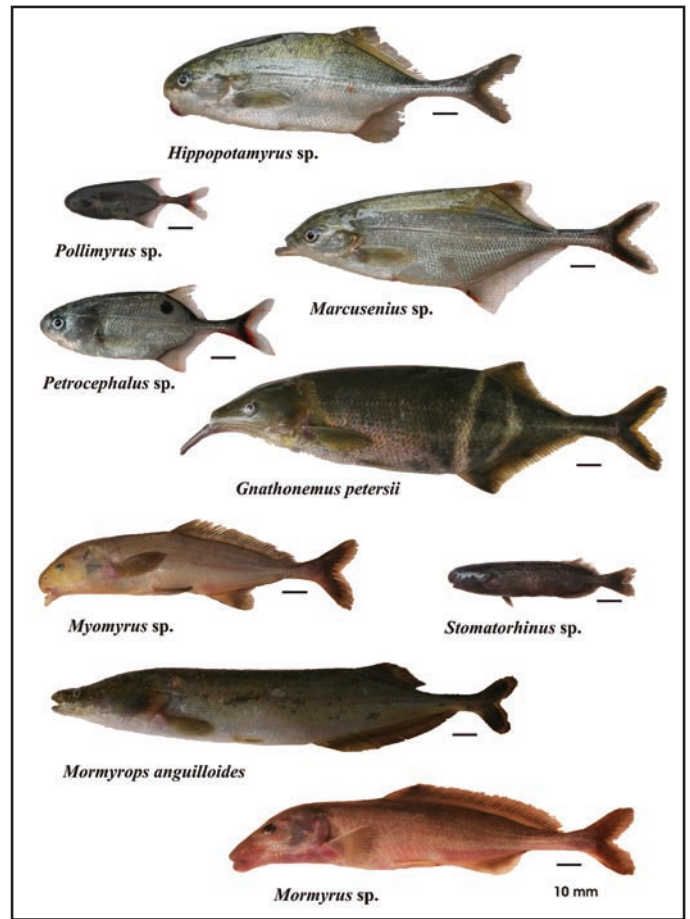


Figure 2. Diversification of snout morphology in the Mormyridae of the lower Congo River.

contrast with studies on various other mormyrid genera where sex-specific differences in the EOD were found—especially during the breeding season.<sup>19-21</sup>

### Electric Mate Choice

Species specificity of EOD types along with the marked differentiation between closely related sympatric species led us to ask whether EOD differentiation affects reproductive isolation.<sup>5,7</sup> In a recent study<sup>18</sup> we showed, using dichotomous choice tests, that sexually mature *Campylomormyrus* females exhibit a preference to associate with conspecific males. Although females could not mate during experiments association preferences, as measured in our study,<sup>18</sup> provides a good proxy to mate choice and has been shown to be a good indicator of mating preferences in other fish species [e.g., blennies (*Salaria pavo*),<sup>22</sup> mollies (*Poecilia mexicana*)<sup>23</sup> and gobies (*Pomatoschistus minutus*)<sup>24</sup>]. Even if the preferences we measured were not entirely sexually motivated, phenotype-assortative social preferences still promote species segregation and thus can facilitate reproductive isolation.<sup>25,26</sup>

Using electric playback experiments we confirmed that female decision-making is indeed based on EOD waveform characteristics.<sup>18</sup> During playback experiments, we kept the amplitude of

EODs and the sequence of pulse intervals (SPI) constant, so any behavioral response in females was due to differences in EOD waveforms. The SPI varies in different contexts, such as foraging, agonistic as well as non-agonistic interactions, while the EOD waveform is determined by the anatomy and physiology of the electric organ.<sup>27,28</sup> Females in our study did discriminate when EOD waveforms differed, preferring the conspecific waveform but did not discriminate between males or playback signals of species with very similar EOD waveforms.<sup>18</sup> Knollenorgan receptors exhibit distinctive responses to different EOD waveforms as shown by a study on the *Paramormyrops* species from Gabon.<sup>29</sup> This indicates that signal discrimination based on EOD waveform characteristics does not require change in receptor response properties.

### Magic Trait EOD

During ecological speciation adaptive trait divergence is caused by disruptive natural selection.<sup>30</sup> Especially in systems, in which diverging morphotypes face gene flow, reproductive isolation is crucial to complete speciation.

Considering the radiation in mormyrid fish, if divergence in snout morphology was the driving force of speciation, then the ecological trait (snout morphology) and traits responsible for

reproductive isolation (EOD waveform) would need to be genetically linked to each other. However, in an alternative scenario where the trait under divergent natural selection is at the same time also responsible for reproductive isolation, e.g., the EOD being adaptive in foraging and simultaneously causing reproductive isolation via assortative mating, no linkage between traits is required. We provide arguments that pronounced differences in EOD both likely affect the food spectrum and are used for mate recognition. Hence, we propose that the EOD of mormyrid fish—with its dual function—could be a “magic trait” combining disruptive natural selection and assortative mating on a single trait.

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