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Species delimitation and phylogenetic relationships in a genus of African weakly-electric fishes (Osteoglossiformes, Mormyridae, *Campylomormyrus*)

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ABSTRACT

African weakly-electric fishes (Mormyridae) are able to communicate through species-specific electric signals; this feature might have favoured the evolutionary radiation observed in this family (over 200 species) by acting as an effective pre-zygotic isolation mechanism.

In the present study we used mitochondrial (*cytb*) and nuclear (*rps7*, *scn4aa*) markers in order to reconstruct a species-phylogeny and identify species boundaries for the genus *Campylomormyrus*, by applying inference methods based on the multispecies coalescent model. Additionally, we employed 16 microsatellite markers, landmark-based morphometric measurements, and electro-physiological analyses as independent lines of evidence to the results obtained from the sequence data.

The results show that groups that are morphologically different are also significantly divergent at the genetic level, whereas morphologically similar groups, displaying dissimilar electric signals, do not show enough genetic diversity to be considered separate species. Furthermore, the data confirm the presence of a yet undescribed species within the genus *Campylomormyrus*.

1. Introduction

Mormyrids are a family of freshwater weakly-electric fishes endemic to African riverine and, partially, lacustrine systems (Daget et al., 1991). They belong to the superorder Osteoglossomorpha, considered as one of the phylogenetically basal nodes of Teleostei (Near et al., 2012). With more than 200 described species in 20 genera, mormyrid fishes account for almost 90% of the overall diversity within living osteoglossomorphs (Lavoué and Sullivan, 2004). Together with their monospecific sister family Gymnarchidae, they share the presence of an electric organ and several electroreceptors which allow them to produce and perceive weak electric discharges (Lissmann, 1958). Most mormyrids are nocturnal, therefore they use their electric sense to actively locate objects and food in the darkness (Bastian, 1994; Lissmann and Machin, 1958; von der Emde, 1999), and for conspecific/mate recognition. Indeed, mormyrids are able to discriminate between conspecific and heterospecific Electric Organ Discharges (EODs), by perceiving differences in waveform shapes and pulse durations (Baker et al., 2013; Bratton and Kramer, 1989; Crawford, 1991; Lamml and Kramer, 2006).

A taxon of mormyrids for which EOD was demonstrated to play a key role in mate recognition and pair formation is the genus *Campylomormyrus* (Feulner et al., 2009a,b; Kramer and Kuhn, 1994). Members of the genus *Campylomormyrus* are characterized by the presence of an elongated trunk-like snout, which may vary dramatically in length and shape across different species (Fig. 1); ecological studies highlighted the link between different snout morphologies and differential feeding habits (Marrero and Winemiller, 1993). Moreover, previous geometric morphometric

Abbreviations: EOD, electric organ discharge; PPS, Posterior Predictive Simulation; PP, posterior probability; MCMC, Markov Chain Monte-Carlo; PCA, Principal Component Analysis; PC, Principal Component; MDS, Multi-Dimensional Scaling.

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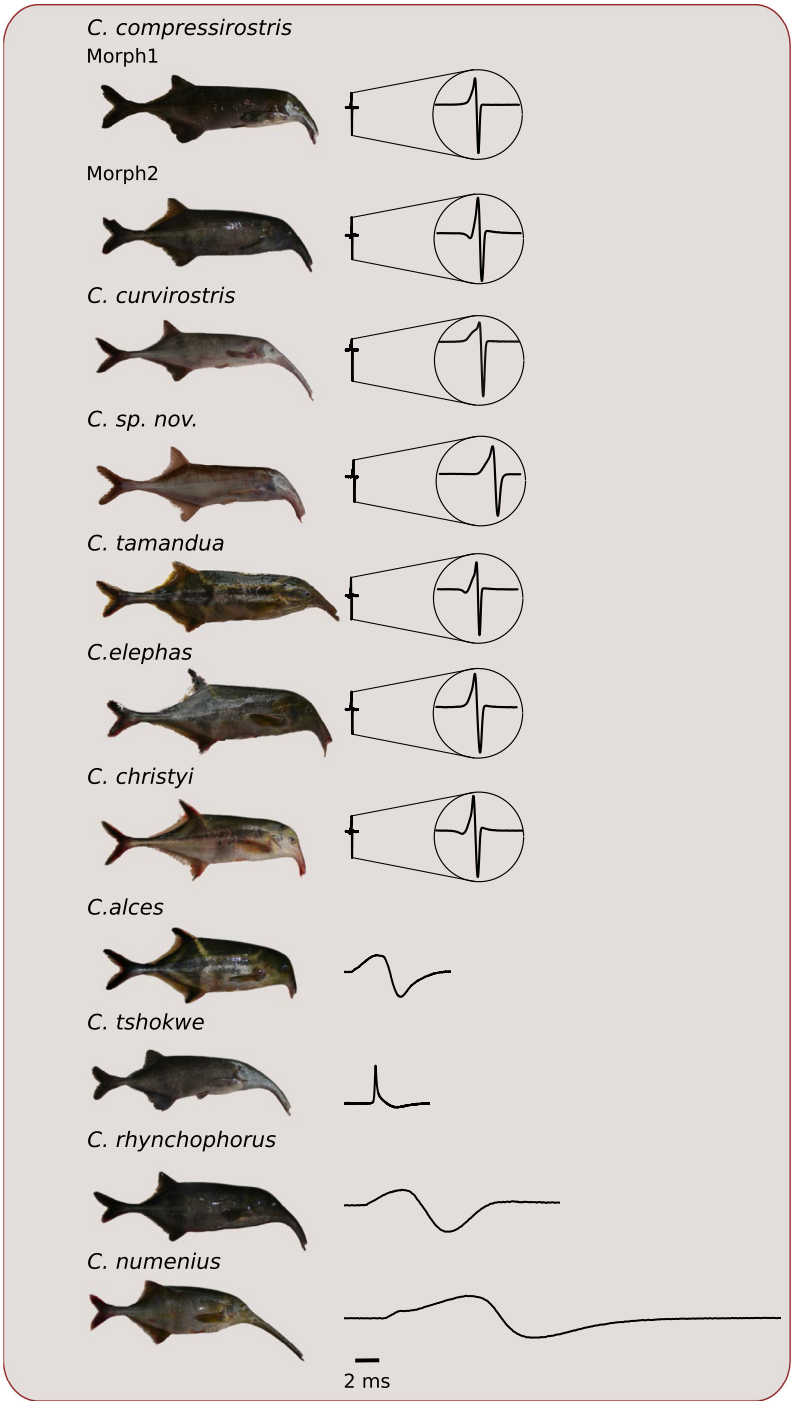

Fig. 1. The species analyzed in this study and their Electric Organ Discharges (EODs). EODs are reported on the same time scale in order to emphasize the pronounced differences in terms of duration in some species. The black bar indicates the time reference in milliseconds. Signals embedded in circles were magnified 10× in order to appreciate their shape features. Morph 1 and 2 belong to *C. compressirostris* and are characterized by two different EOD waveforms (biphasic vs. triphasic). *C. alces*, *C. elephas*, and *C. christyi* belong to the so-called "*alces*" species-complex.

analyses showed that most of the morphological variance among different species is confined within the snout region (Feulner et al., 2008, 2007). Both lines of evidence invoke ecological adaptation as the main factor that might have prompted speciation within this genus in sympatry. Alongside of morphological divergence, *Campylomormyrus* species display very remarkable differences in terms of EOD shape and duration (Fig. 1). All members of the genus except two (*C. tamandua*, *C. phantasticus*), occur exclusively in water bodies within the Congo basin, with peaks of diversity observed in the rapids of the lower Congo region (Roberts and Stewart, 1976). The most recent taxonomic revisions of the genus (Feulner et al., 2007; Poll et al., 1982) acknowledged 15 species, however this is likely an underestimate of the actual *Campylomormyrus* diversity, since many areas of the Congo basin have not been explored yet.

Previous molecular phylogenies of the genus (Feulner et al., 2006, 2007) confirmed that several described species, which are distinct in terms of morphology and EOD shape and length, constitute monophyletic groups. However, the inferred trees showed lack of resolution for two morphologically distinct taxa