PHYLOGENETIC OCCURRENCE OF ELECTRORECEPTION AND BIOELECTROGENESIS IN TELEOST FISH:

EXAMPLES OF CONVERGENT EVOLUTION

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EXTENDED ABSTRACT ONLY – DO NOT CITE

Electric fields in the water can play a major role in the biology of fish through two main biologically relevant circumstances: some fish are able to detect electric gradients in the surrounding medium through a set of specialized sensorial cells, and some fish possess specialized organs that generate electric discharges on a more or less regular basis.

For those fish possessing both Electrosensory and Electrogenic Systems (EES), the electric field generated during an Electric Organ Discharge (EOD) is monitored by an array of electroreceptors distributed over the fish's skin. The two systems working in tandem constitute an effective sensory-motor "unit" that is particularly important for electrolocation and communication. Despite the obvious benefit of having both systems, bioelectrogenesis and electroreception do not always co-occur in the teleosts. There are electroreceptive fish that do not possess electric organs, and there is at least one species of electrogenic teleost (family Uranoscopidae) that has no electroreceptive capability (Bullock et al., 1983).

Electroreceptors can be broadly divided into ampullary and tuberous types according to their morphological and physiological properties. Ampullary electroreceptors detect DC fields and low frequency AC fields. According to the phylogeny of the clades involved and parsimony analysis of character evolution, this type of receptor evolved only within two distantly related fish groups: once in the common ancestor of Notopteriformes + Mormyriformes (superorder

Osteoglossomorpha), and a second time in the common ancestor of Siluriformes + Gymnotiformes (superorder Ostariophysi). The second class, the tuberous electroreceptors, are physiologically most sensitive to the dominant frequencies of the fish's own EOD (Zakon, 1986), and was thought to have evolved twice among teleosts, more specifically only in those clades that also have electric organs: the South American order Gymnotiformes and the African order Mormyriformes. However, a tuberous electroreceptor has been described for *Pseudocetopsis*, a South American catfish of the family Cetopsidae (Andres et al. 1988). Therefore, tuberous organs have evolved independently in three teleost lineages: mormyriforms, gymnotiforms and *Pseudocetopsis*.

Electric organs evolved eight times among teleosts, and five times within the superorder Ostariophysi alone. In the osteoglossomorphs, it is assumed that an electric organ was present in the common ancestor of all mormyriforms. Within the ostariophysans, electric organs evolved in the gymnotiforms' common ancestor and in four siluriform genera: *Clarias*, *Malapterurus*, *Auchenoglanis* and *Synodontis*. The other teleosts possessing an electric organ are *Astroscopus* and *Uranoscopus*, two genera of the perciform family Uranoscopidae (Moller, 1995). Systematic studies (Pietsch, 1989) and morphological examination of the electric organ in the two uranoscopids suggest that they are not homologous. In summary, electric organs appear to have evolved independently in the following teleost lineages: 1) Mormyriformes, 2) Gymnotiformes, 3) *Synodontis*, 4) *Clarias*; 5) *Malapterurus*, 6) *Auchenoglanis*; 7) *Astroscopus*, and 8) *Uranoscopus.*

As one maps the evolution of electric organs and electroreceptors onto teleost phylogeny it is possible to note that, with exception of the uranoscopids, all electric organs evolved in fish that already were electroreceptive. Further, the plesiomorphic electroreceptive teleost lineages had only ampullary organs, as tuberous electroreceptors evolved later in few select electrogenic groups. The development of active electrolocation (an electric organ) on top of an already existing electroreceptive capability likely represents, in terms of costs and benefits, a relatively minor step for a great reward. Because ampullary receptors are physiologically tuned to low-frequency AC and DC signals, in the beginning there must had been a real evolutionary advantage for signals that matched the electroreceptors' tuning curve, suggesting that plesiomorphic waveforms were composed of low-frequency signals such as long lasting monophasic discharges. The development of multiphasic, complex EOD waveform was probably the best evolutionary option to solve some significant limitations of monophasic pulses. First, it allowed a larger number of possibilities in terms of waveforms, supporting species specificity. Second, by adding fast-frequency components in the EOD, fish were able to broaden the spectral frequency of their discharges, improving the efficiency with which they use their EES to probe the environment. Third, fast frequencies components can shift the spectral peak power frequency of the EODs above ampullary thresholds of electroreceptive predators such as catfishes.

The EOD waveform is the result of complex interaction of several physiological and anatomical features associated with the fish's electric organ. Nonetheless, EODs tend to be a plastic character because they are under constant selective pressure to evolve an ideal compromise between a trait that enhances electrolocation and electrocommunication, ensures species identity through sexual and behavioral segregation, and minimizes the risk of predation.

References

Andres, K. H., D. M. von, and E. Petrasch. 1988. The fine structure of ampullary and tuberous electroreceptors in the South American blind catfish Pseudocetopsis spec. *Anat Embryol (Berl)*, 177:523-35.

Bullock, T. H., D. A. Bodznick, and R. G. Northcutt. 1983. The phylogenetic distribution of electroreception: Evidence for convergent evolution of a primitive vertebrate sense modality. *Brain Res. Rev.*, 6: 25-46.

Moller, P. 1995. *Electric Fishes - History and Behavior*. Chapman & Hall, London.

Pietsch, T. W. 1989. Phylogenetic relationships of trachinoid fishes of the Family Uranoscopidae. *COPEIA*, 1989:253-303.

Zakon, H. H. 1986. The electroreceptive periphery. In T. H. Bullock and W. Heiligenberg (eds.), *Electroreception*, pp. 103-156. John Wiley & Sons, New York.