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Family Mormyridae: Form, Function, Phylogeny, Evolution, and Comparison

Introduction

The family Mormyridae, order Mormyriformes, is comprised of the weakly electric fish found in the African freshwaters. This family of fish is exclusively found in Africa and can be found in almost every body of freshwater south of the Sahara (Hopkins, 1986). Their habitats range from bottom dwellers to top feeders of deoxygenated swamps to swift rapids (Hopkins, 1986). Although the types of habitats are diverse, most contain suspended particles, making the water murky (Moyle and Cech, 2000).

Mormyrids are known for their characteristic electrogenic and electrosensory systems (EESs). All fish in this family produce weak electric discharges by a highly specialized organ in the tail (Hopkins, 1986; Hopkins, 1981). Mormyrids can use their EESs for communication; location of objects, prey, obstacles, and boundaries; and courtship (Bullock, 1986; Crawford and Huang, 1999). An ability in several marine and freshwater fish (**Fig. 1**), electroreception may be used to give orientation clues, since water and fish moving through the earth's magnetic field produce electric fields (Kalmijn, 1974). Although electroreception is not exclusive to mormyrids, they may be unique among vertebrates in having this unique sense organ used primarily for sensing communication signals (Hopkins, 1986).

The unique capabilities of the mormyrids with their unique sensing organs, begs the question of why did it develop in the first place? How did the mormyrids evolve, and possibly more interesting, how did their unique EESs evolve? This paper will attempt to address these questions.

Mormyrid Electrogenic and Electrosensory Systems

Electrogenic

The mormyrid electrogenic system relies on specially adapted muscles, found in the electric organ, called electrocytes (Dye and Meyer, 1986). The electric organ, located near the tail, consists of two columns of disk-shaped electrocytes on each side of the spinal chord which are serially stacked (**Fig. 2**) (Bass, 1986). Electrocytes can have either penetrating or non-penetrating stalks, referring to which face (anterior or posterior) the finger like evaginations (stalks) are innervated by electromotor neurons (Bass, 1986). Penetrating stalks penetrate the electric body on the posterior face and emerge on the anterior side (**Fig. 2**) (Bass, 1986). With the exception of species of the genus *Pollimyrus*, mormyrid species exhibit only one type of stalk penetration or the other (Sullivan, et al., 2000). Species with non-penetrating stalks produce simple biphasic electric organ discharge (EOD) waveforms, while species with penetrating stalks produce more complicated EOD waveforms (Sullivan, et al., 2000). It is interesting to note that most species with non-penetrating stalk electrocytes are found in rivers, while most with penetrating stalks are found in streams, (Bass, 1986).

The EOD can span from 1-2 m from the fish and varies in duration, number, and amplitude of peaks. They also vary in polarity and wave shape (Sullivan, et al., 2002). Electrocytes of the electric organ have resting potentials of 60-80 mV and can generate spikes of 80-130 mV (Bass, 1986). The electrocytes are controlled in three ways: by electromotor neurons in the spinal chord, the medullary relay nucleus in the brainstem, and the pacemaker nucleus (which fires one-for-one with the electric organ) (Dye and Meyer, 1986).

Interestingly, sex can have an effect on the EOD. In many species, male and female EODs differ during breeding season (Sullivan, et al., 2002). The males will have EOD pulses lasting 2-3 times as long as female EOD pulses (Hopkins, 1986). It appears that hormones are involved with this regulation (Bass, 1986).

Electrosensory

The electrosensory system of mormyrids consists of ampullary receptor organs and two distinct tuberous receptor organs called knollenorgans and mormyromasts (Zakon, 1986). Ampullary receptor organs contain receptors which are able to detect low frequency electric fields (Zakon, 1986). They are associated with passive electrolocation and are useful in prey detection and predator avoidance (Bell and Szabo, 1986; Hopkins, 1986).

Knollenorgans are tuberous with each of its receptor cells enclosed in its own capsule. These receptor cells function to signal the occurrence of EODs from other fish and are capable of firing a single spike (to the brain) locked to the EOD pulse (Zakon, 1986). Knollenorgans are associated with electrocommunication and social interaction (Bell and Szabo, 1986; Hopkins, 1986).

Mormyromasts, on the other hand, consist of two sensory cell types with one embedded in the epithelium and one projecting into the interior of a deeper chamber. They function to code the EOD pulse amplitude (normally the fish's own EOD) (Zakon, 1986). Mormyromasts are involved in active electrolocation (Bell and Szabo, 1986). See **Table 1** for a summary of the above information.

There are ten mormyromasts for every knollenorgan (Zakon, 1986). Tuberous receptor organs are capable of tuning to different frequencies. This is important for filtering out background noise, "listening" to fish of the same species, and tuning into calls from the opposite sex (Zakon, 1986).

Active electrolocation involves the perception and interpretation of changes in an ambient electric field (Dye and Meyer, 1986). As a result, mormyrids are capable of discriminating between non-conducting materials such as rocks and conductors such as plants and larvae (von der Edme and Bleckmann, 1998). To make the electrolocation process easier, mormyrid fishes have rigid body postures with locomotion generated by undulation of long dorsal fins (Moyle and Cech, 2000).

Phylogeny

Mormyrids are members of the most primitive group of living teleosts (**Fig. 3**), the Osteoglossomorpha (bony tongued) fishes (Hopkins, 1986). Of the 220 known osteoglossomorphs, 200 belong to the Mormyridae family (Moyle and Cech, 2000). It is thought, however, that the osteoglossomorphs were once the dominant group of the freshwater fauna prior the ostariophysan fishes (Moyle and Cech, 2000).

The order Mormyroformes (**Fig. 4**) contains two main clades: the family Mormyridae and the family Gymnarchidae (Alves-Gomes, 1999; Sullivan, et al., 2002). Gymnarchids are the most primitive group of Mormyriformes because their electrocytes have no stalks and the posterior face is innervated by spinal axons (Bass, 1986). The sister-group of the mormyriforms, the notopteriforms (**Fig. 4**), likely evolved after the separation of Africa and South America 84 to 112 MYA (Alves-Gomes, 1999).

When looking at the family Mormyridae itself, phylogenetic trends are difficult to find because electrocyte morphology varies at the species level (Bass, 1986). The family Mormyridae can still be divided into two subfamilies: Petrocephalinae and Mormyrinae (Hopkins, 1986; Alves-Gomes, 1999). Recent technology has aided in further phylogenic analysis. New clades within Mormyrinae have recently been found (Sullivan, et al., 2002).

As of 1999, fossil records of mormyriforms are non-existent (Alves-Gomes, 1999). Based on the fossil record available for analysis, the minimum separation time for the divergence of the Osteoglossomorpha from the other teleosts was 144 to 163 MYA (Alves-Gomes, 1999). If the fossil *Ostariostoma*, from the Late Crustaceous- Early Paleocene era, is the sister group of the clade Notopteriformes + Mormyriformes, then the ancestral lineage that later differentiated into those two groups was in existence in the Early Paleocene period (62.3 to 66.4 MYA) (Alves-Gomes, 1999). If this is true, it implies that the two lineages evolved after the separation of South America from Africa which occurred anywhere between 144 and 163 MYA (Alves-Gomes, 1999). The separation from Pangea/Gondwana likely played role in the divergence of South American Gymnotiformes (electric fishes with similar EESs).

Evolution

It would be difficult to discuss the evolution of mormyrids without discussing the evolution of their characteristic EESs as well. Ad. Kalmijn's suggestion, that perhaps the motional electric fields played a role in the evolution of deep sea and shore life, is not a common evolutionary pressure to think about (1974). Electroreception, as mentioned, is not exclusive to mormyrids (Bass, 1986). Groups of elasmobranch fishes (such as sharks, skates, and rays) and groups of siluriform fishes (such as catfish) are able to sense electrical fields (Bass, 1986). Theodore Bullock believes that electrorecption must have been a sense evolved in some ancestor of the agnathan and cartilaginous fishes (1986). In the teleosts, electroreception appears to have evolved independently in two lineages: the siluriform/gymnotiform line and osteoglossomorph line (Finger, et al., 1986).

Many factors may have influenced the evolution of the electric organ, so it is not a surprise that no single selective pressure can account for its evolution (Bass, 1986). Electric organs have evolved at least six times (Zakon and Unguez, 1999). They evolved from different striated muscles in different lineages including tail muscles, axial muscles, and oculomotor muscles (Zakon and Unguez, 1999). Electrocyte evolution is the result of several regressive specializations (Bass, 1986). Although the contractile elements and the excitation-contraction coupling process of muscle are gone or disabled, remnants of the striated muscle fibers found in the electrocyte include myofibrils and vestigial tubules of the sarcoplasmic reticulum (Bass, 1986; Zakon and Unguez, 1999).

Sullivan et al. suggest that penetrating stalk electrocytes evolved once in the evolutionary history of mormyrids (2000). They go on to suggest that electric organs with non-penetrating stalks are the result of multiple independent reversals to the ancestral condition (Sullivan, et al., 2000). This implies that penetrating electrocyte stalks are the primitive condition for the family Mormyridae. Assuming that the first mormyrids used their EOD for both communication and location, the fish with penetrating stalks were likely effective in several ways. Penetrating stalks reduce the DC components of the fish's own EOD which allows the fish to prevent jamming itself as well allowing itself to keep a low profile against DC sensitive catfish predators (Sullivan, et al., 2000). Fish with penetrating stalks may produce EODs with a higher frequency which would have made use of the less used bandwidth (Sullivan, et al., 2000). Fish with penetrating stalks may also be able to produce more complex EOD waveforms useful in recognition and reproduction isolation (Sullivan, et al., 2000). Fish with non-penetrating stalks (reversal to the ancestral condition), may have a relaxed bandwidth (Sullivan, et al., 2000).

Not only have electrocytes and electric organs evolved, but the EOD has evolved as well . Like electroreception and the electric organ, the EOD likely evolved due to several different evolutionary pressures. EOD diversity in mormyrids may be related to changes in the detailed morphology and geometry of the electrocytes of the electric organ (Bass, 1986). The presence of background noise in the environment from non-biological sources could have also influenced the evolution of the EOD (Hopkins, 1981). Social or competitive interaction between fish may have been a factor. Similar EODs cause jamming, therefore the unique EOD of a species may have evolved as a result (Dye and Meyer, 1986).

It is uncertain whether the EESs adapted at the same time, but looking at the structure of the mormyrid brain may reveal some clues. The relative brain weight of the mormyrid, *Gnathonemus petersii*, is 3.1% of its total body weight and exceeds that of other fishes (<1% of body weight) and even humans (2.3% of body weight) (Moyle and Cech, 2000). The brain of *G. petersii* is so large and active that it consumes 60% of the total oxygen requirement for the animal (Moyle and Cech, 2000). The large relative brain weight may indicate coadaptation of the electric organ, active electrosensory system, and the central nervous system (Bass, 1986).

Comparative EESs

An order of fish with similar electric capabilities as the mormyriforms is the order Gymnotiformes of South America. While both orders have fish with electric capabilities, it has been established that gymnotiforms and mormyriforms evolved their EESs independently of each other (Alves-Gomes, 1999). Gymnotiformes, of the superorder Ostariophysi, and Mormyriformes, of the superorder Osteoglossomorpha (bony tongues), are both of the division Teleostei. The two teleosts clades are widely separated within the evolutionary history of fishes (Alves-Gomes, 1999). Looking at the oldest fossil assigned to osteoglossomorphs, gymnotiforms and mormyriforms have been separated for at least 140 million years (Alves-Gomes, 1999). By looking at genetic distances among the Mormyriformes and comparing them with those of the Gymnotiformes, the Mormyriformes clade is the younger of the two (Alves-Gomes, 1999).

The two teleosts electroreceptive systems are very similar in some aspects. Gymnotiform and mormyriform electroreceptors are excited by the onset of outside-positive stimuli (Finger, et al., 1986). Behaviorally, both gymnotiform and mormyriform fishes show probing behavior when exploring objects. Both fish families back up to objects presumably trying to maximize distortion of their electric field by the object (Finger, et al., 1986). Also, species in both families exhibit sexually dimorphic EODs (Finger, et al., 1986).

Electroreception is not just limited to fish. A German-Australian joint team of researchers in 1986 discovered electroreception in the monotreme, *Ornithorhynchus anatinus* (commonly called the duck-billed platypus) (Pettigrew, 1999). *Tachyglossus aculeatus* and *Zaglossus bruijni* (short and long beaked echidna, respectively) were soon found to have electroreceptors as well (Pettigrew, 1999). The electroreceptive systems in fish and monotremes are similar in a number of ways. The threshold field strength for the platypus is similar to the sensitivity of the mormyriforms and gymnotiforms (Pettigrew, 1999). Similarities include electroreceptor pore length, secretion filled canals for better electrical conduction, the passive use of electroreceptors to find food, and the ability to judge distances (Manger and Pettigrew 1996; Pettigrew 1999).

Despite the similarities, there are a many important differences between platypus and fish electroreception. In fish, the electroreceptive apparatus is innervated by the octavolateralis system, whereas in the platypus, the electroreceptive apparatus is innervated by the trigeminal nerve (Manger and Pettigrew 1996). Electroreceptive fish have receptors on their entire body while platypus receptors are located exclusively on the bill (Manger and Pettigrew 1996).

Closing Remarks

The family Mormyridae represents a very interesting and diverse group of freshwater fish that independently evolved a complex electrogenic and electrosensory system. Their ability to use their EESs for communication; location of objects, prey, obstacles, and boundaries; and courtship makes them unique when compared animals with similar form and function.

Literature Cited

Alves-Gomes, J. A. 1999. Systematic biology of gymnotiform and mormyriform electric fishes: Phylogenetic relationships, molecular clocks and rates of evolution in the mitochondrial rRNA genes. *Journal of Experimental Biology* 202: 1167-1183.

Bass, A. H. 1986. Electric organs revisited: Evolution of a vertebrate communication and orientation organ. In Bullock, T. H. and Heiligenberg, W. [eds.], *Electroreception*, p 13-70. John Wiley and Sons, New York, NY.

Bell, C. C. and Szabo, T. 1986. Electroreception in mormyrid fish: Central physiology. In Bullock, T. H. and Heiligenberg, W. [eds.], *Electroreception*, p 375-421. John Wiley and Sons, New York, NY.

Bullock, T. H. 1986. Significance of findings on electrorecption for general neurobiology. In Bullock, T. H. and Heiligenberg, W. [eds.], *Electroreception*, p 651-674. John Wiley and Sons, New York, NY.

Crawford, J. D. and Huang, X. 1999. Communication and sound production mechanisms of mormyrid electric fish. *Journal of Experimental Biology* 202: 1417-1426.

Dye, J. C. and Meyer, J. H. 1986. Central control of the electric organ discharge in weakly electric fish. In Bullock, T. H. and Heiligenberg, W. [eds.], *Electroreception*, p 71-102. John Wiley and Sons, New York, NY.

Finger, T. E., Bell, C. C. and Carr, C. E. 1986. Comparisons among electroreceptive teleosts: Why are electrosensory systems so similar? In Bullock, T. H. and Heiligenberg, W. [eds.], *Electroreception*, p 465-481. John Wiley and Sons, New York, NY.

Hopkins, C. D. 1981. On the diversity of electric signals in a community of mormyrid electric fish in West Africa. *American Zoologist* 21: 211-222.

-----------------. 1986. Behavior of Mormyridae. In Bullock, T. H. and Heiligenberg, W. [eds.], *Electroreception*, p 527-576. John Wiley and Sons, New York, NY.

Kalmijn, Ad. J. 1974. The detection of electric fields from inanimate and animate sources other than electric organs. In Fessard, A. [ed.], Electroreceptors and other specialized receptors in lower vertebrates, p 147-200. Springer-Verlag, Berlin.

Manger, P. R., and Pettigrew, J. D. 1996. Ultrastructure, number, distribution and innervation of electroreceptors and mechanoreceptors in the bill skin of the platypus, *Ornithorhynchus anatinus*. *Brain Behavior and Evolution* 48: 27-54.

Moyle, P. B. and Cech Jr., J. J. 2000. Fishes: An introduction to ichthyology, Fourth Edition. New Jersey: Prentice Hall. 612 p.

Pettigrew, J. D. 1999. Electroreception in monotremes. *Journal of Experimental Biology* 202: 1447-1454.

Sullivan, J. P., Lavoué, S. and Hopkins, C. D. 2000. Molecular systematics of the African electric fishes (Mormyridae: Teleostei) and a model for the evolution of their electric organs. *Journal of Experimental Biology* 203: 665-683.

-----------------. 2002. Discovery and phylogenetic analysis of a riverine species flock of African electric fishes (Mormyridae: Teleostei). *Evolution* 56: 597-616.

von der Edme, G. and Bleckmann, H. 1998. Finding food: Senses involved in foraging for insect larvae in the electric fish *Gnathonemus petersii*. *Journal of Experimental Biology* 201: 969-980.

Zakon, H. H. 1986. The electroreceptive periphery. In Bullock, T. H. and Heiligenberg, W. [eds.], *Electroreception*, p 103-156. John Wiley and Sons, New York, NY.

Zakon, H. H and Unguez, G. A. 1999. Development and regeneration of the electric organ. *Journal of Experimental Biology* 202: 1427-1434.

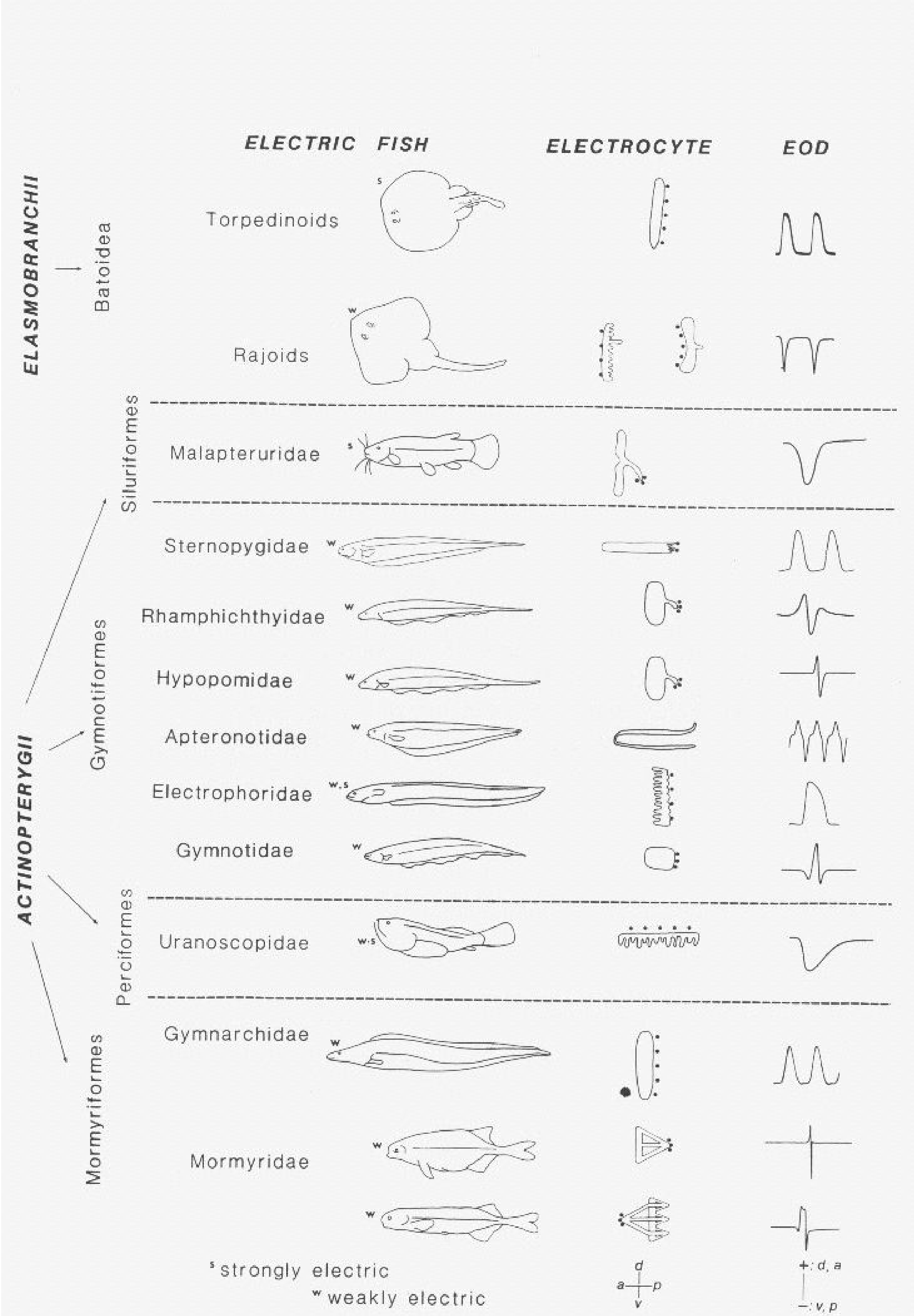

Figure 1. The electric fish of classes Actinopterygii and Elasmobranchii. Taxonomic orders are listed vertically, and family names are listed horizontally. The center cartoon shows the shape and innervations of the electrocytes. This figure is taken from Bass (1986).

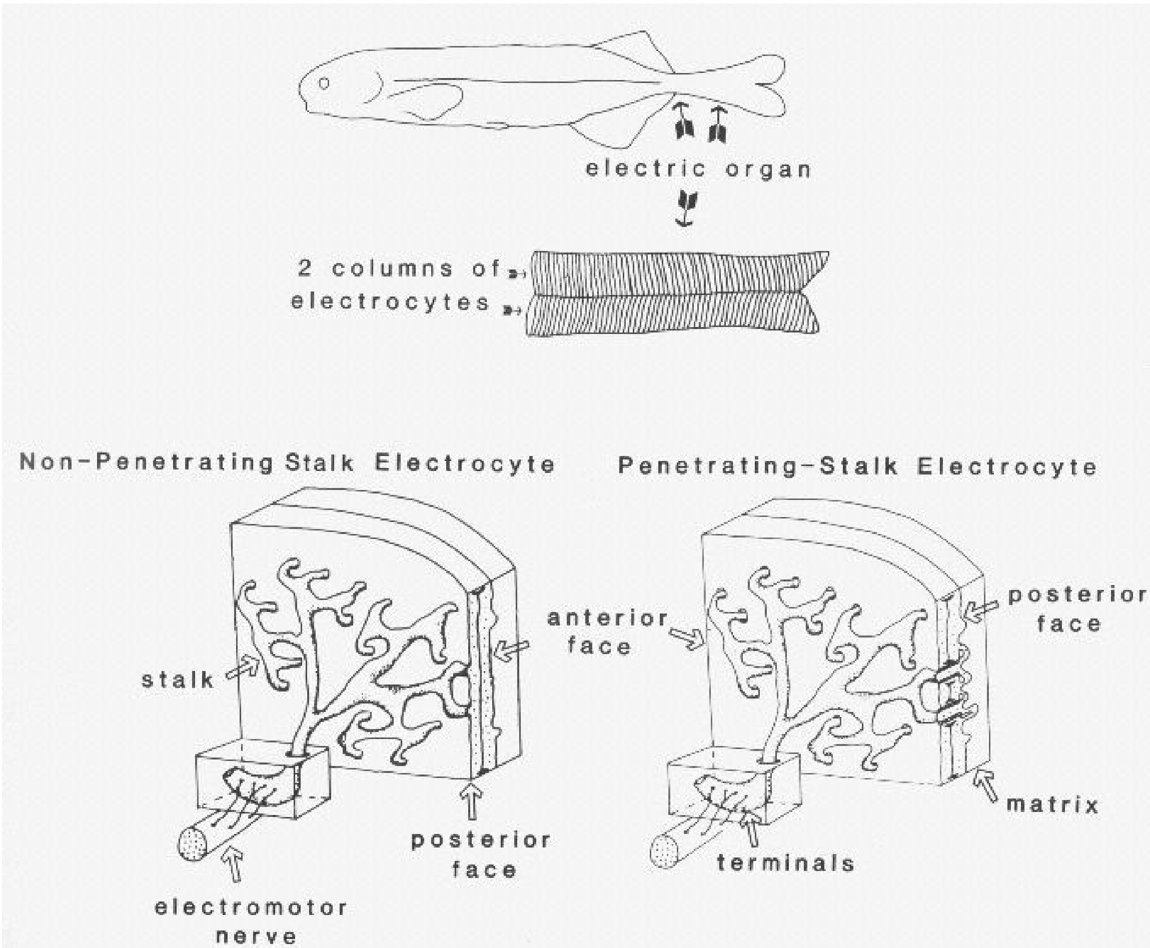

Figure 2 The electric organ of mormyrids. The two morphological patterns, penetrating and non-penetrating stalk electrocytes are shown as well. This figure is taken from Bass (1986).

Table 1. Summary of the electrosenory organ type and its function in the electrosensory system. (Bell and Szabo, 1986; Hopkins, 1986)

Receptor Organ	**Function**
Knollenorgan	electrocommunication/social interaction
Mormyromast	active electrolocation
Ampullary	low frequency passive electrolocation/prey detection/preditor avoidance

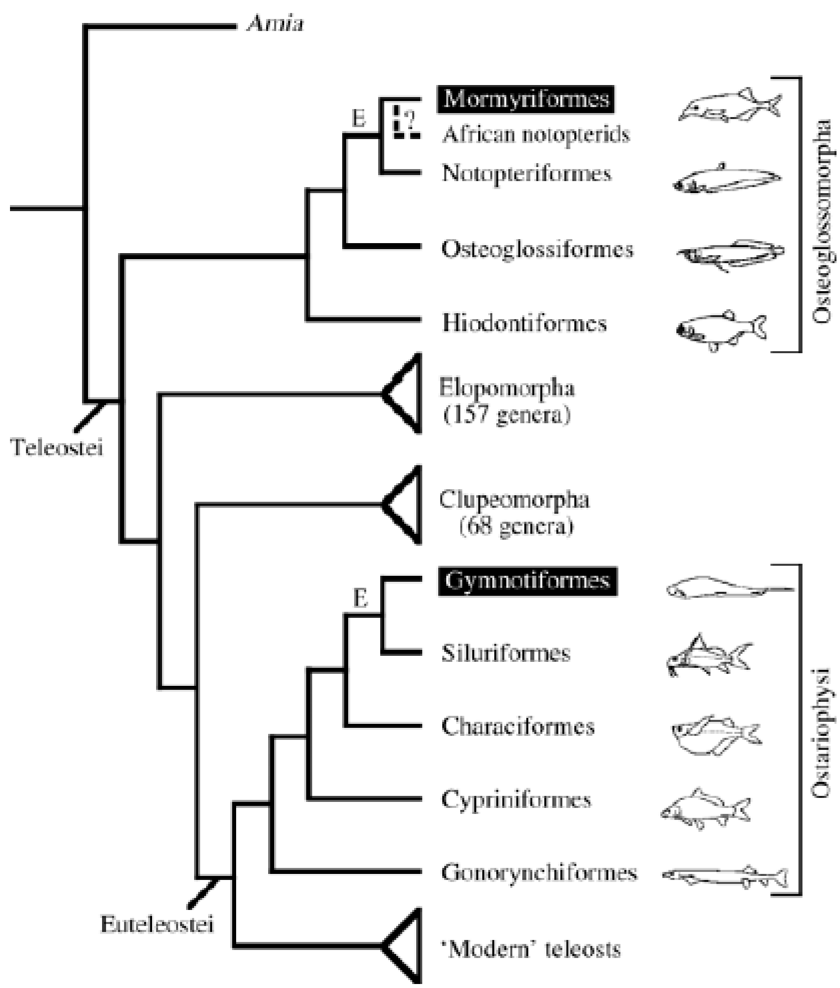

Figure 3. The phylogeny of division Teleostei. The order names are listed at the end of the appropriate clades. The top highlighted term is Mormyriformes, and the lower highlighted term is Gymnotiformes. Shown here are two superoders: Osteoglossomorpha and Ostariophysi. Taken from Alves-Gomes (1999).

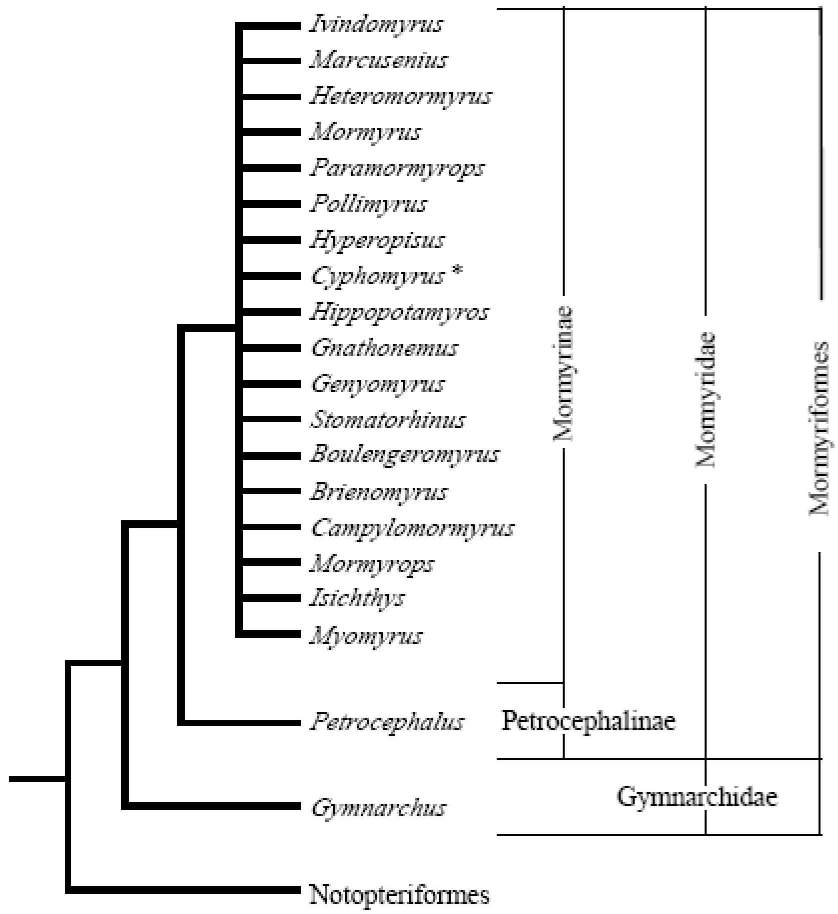

Figure 4. The phylogeny of order Mormyriformes. Taken from Alves-Gomes (1999).