to the spectral properties of the electric organ discharge (usually of much higher frequencies than present in ambient electric fields); and (iii) huge brains with specialized areas and somatotopic maps for complex computations on the sensory feedback (reafference) received from autostimulation. In its function and complexity, this system is comparable to the echolocation, or SONAR, system of many bats; however, the reach of this active electric system is severely limited by physical constraints.

A weakly electric fish detects the presence of an object when it distorts the geometry of the electric dipole field the fish generates with each electric organ discharge (Fig. 5).

Nonconducting objects, such as stones, force the electric current to pass around, whereas conducting objects (such as live organisms) attract the electric current. Therefore, a local decrease of resistivity (relative to the tropical freshwater of high resistivity) causes the current passing through the fish's skin next to the object to increase (for conductors), whereas a local increase in resistivity causes a decrease (for nonconducting objects). The tuberous receptor organs embedded in the skin faithfully reflect these changes in the strength of reafference from autostimulation. Receptor organ position on the fish's body and receptor response pattern are mapped to the brain. In mormyrids, active electrolocation is mediated by tuberous receptor organs termed mormyromasts rather than Knollenorgan, in gymnotiforms, it is probably both types of tuberous electroreceptor organs that are involved (B and M units for pulse fish, T and P units for wave fish). In addition to the resistive impedance properties of an object, an electric fish may also detect its capacitive impedance (if present). As long as they are alive, all organisms have considerable capacitive properties that filter the discharge in phase, waveform and spectral properties, making it thus detectable for the fish [10].

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E

Electric Field

Definition

A space-filling force field around every electric charge or group of charges.

►Electric Fish

Electric Fish

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Synonyms

Electrogenic fish

Definition

Some fishes possess electric organs who's only known function is the generation of electricity outside their bodies. Strong organs are for defense and stunning prey, weak organs for active electrolocation and electrocommunication in nocturnal species.

Characteristics

For more detailed reviews, see [1–3]. Any living tissue generates an electric field in its environment. The field is associated with the regulation of the tissue's ionic balance. These fields are D.C. or of low frequency, and, in animals, usually modulated by superimposed field potentials arising from normal nerve and muscle cell activity. Relative to a distant electrode, potentials measured are up to 0.5 mV in marine species, and a few Millivolt in freshwater teleosts (see entry "►electric communication and electrolocation").

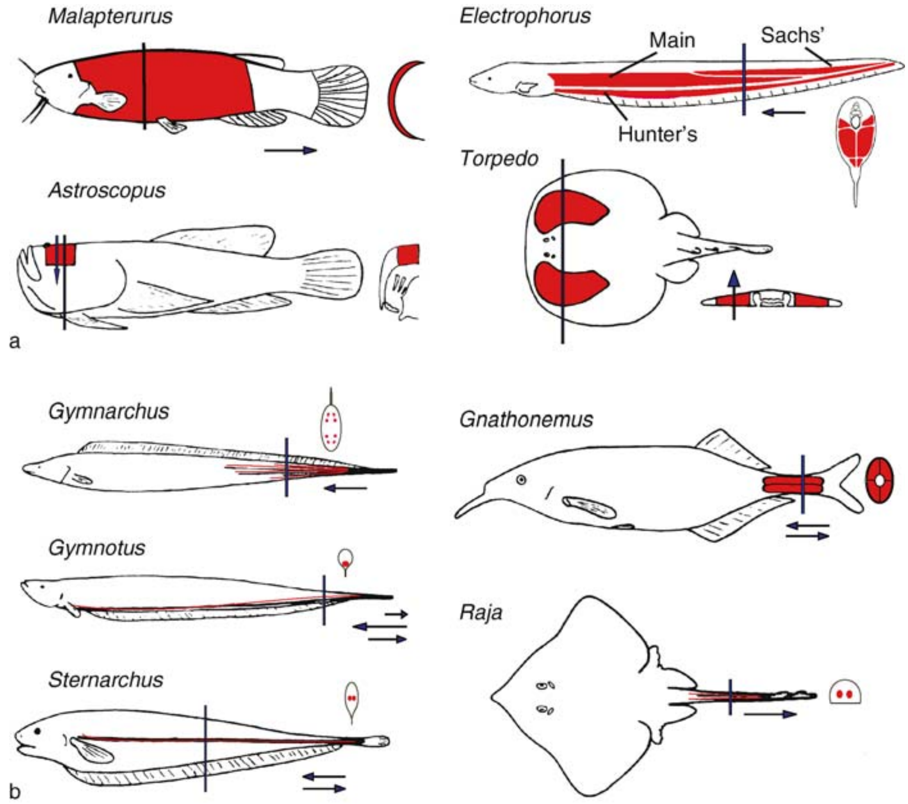
In electric fishes, however, the generation of electricity is of another dimension, both in amplitude and regularity. These fishes' electric organs are anatomically and physiologically specialized to generate electric organ discharges [4]. Electric organ discharges are precisely controlled in waveform, amplitude and frequency; electric organ discharges are species-characteristic and have even been used to tackle systematic and taxonomy problems. The electric organs are under the exclusive control of the brain [4]. The electric fields generated range from very weak (similar to the magnitude of incidental stray fields) to very strong (greater than 500 V).

All electrogenic species, except the stargazers, are also electroreceptive, and carry electroreceptor organs of at least one kind [5].

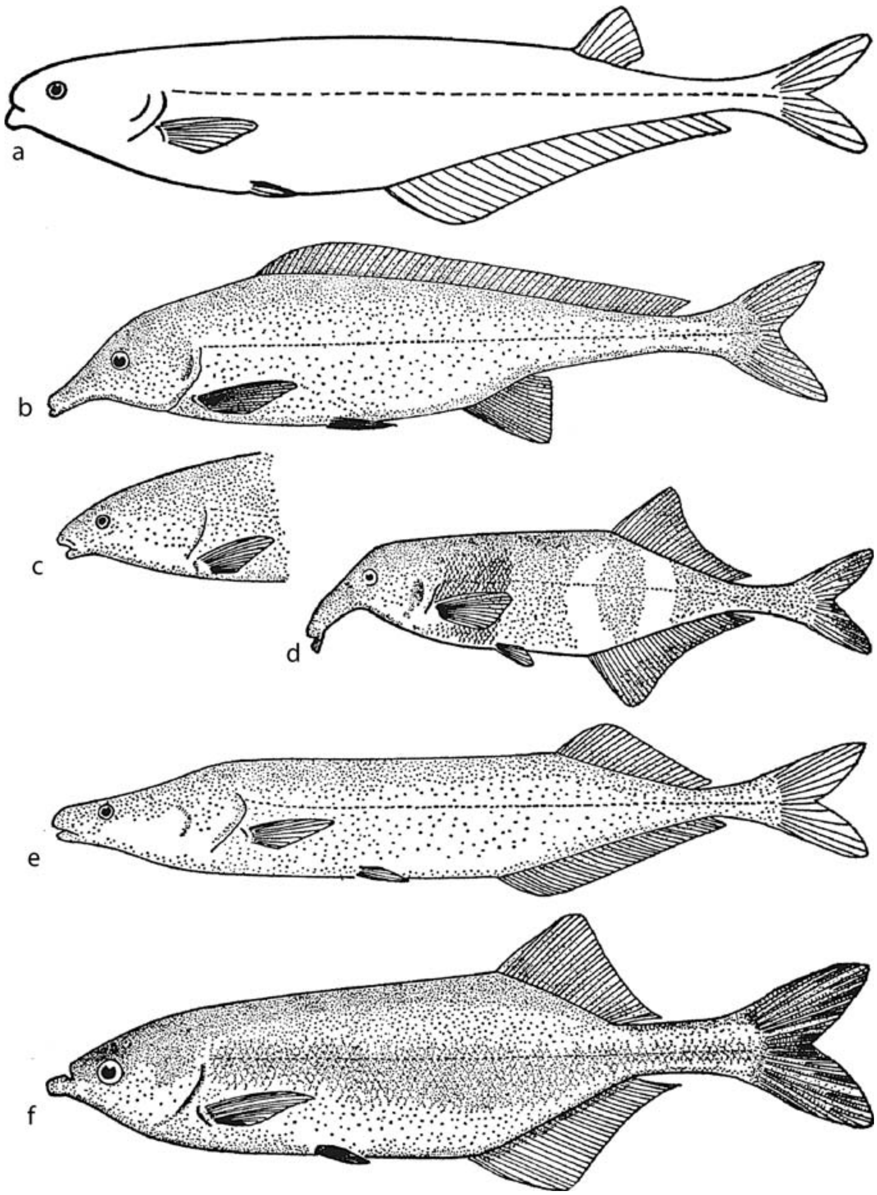
Phylogeny

In the whole animal kingdom, it is only among two classes of jawed aquatic vertebrates (Pisces) that we find electrogenic members: the cartilaginous and the bony fishes (Chondrichthyes and Osteichthyes, respectively; Fig. 1).

Within the cartilaginous fishes, only some rays (Batidoidimorpha) have electric organs; these include the weakly electric skates (190 species of Rajidae) and the exclusively marine, strongly electric rays (38 species of Torpedinidae). Among the bony fishes, it is only in four among the many orders and suborders of teleosts that we find electrogenic members. All of these are tropical freshwater fish, with the exception of the marine stargazers (3 species among the perches or Perciformes that are rather "weak" strong electric fish). The electrogenic tropical freshwater fish include the Mormyriformes, the African weakly electric snoutfishes (about 200 species; Fig. 2); the Gymnotiformes,



Electric Fish. Figure 1 Schematically represented electric fish and their organs. (a) Strongly electric, (b) weakly electric. All are shown from the side except *Torpedo* and *Raja*, which are shown from the top. Electric organs shown by *color*. Cross-sectional plane as indicated by *line*. The *arrows* indicate the direction and sequence of current flows through the organs; the length of these arrows is proportional to the amplitude of the successive phases (if there is more than one). *Raja* and *Torpedo* species are cartilaginous fishes, all other fishes are bony fishes (subdivision teleosts). *Astroscopus,* several species of stargazers, are perches; *Malapterurus electricus*, the electric catfish; *Gnathonemus sp.*, a snoutfish, and *Gymnarchus niloticus* are Mormyriforms; *Electrophorus electricus*, the electric eel, *Gymnotus sp.* and *Sternarchus sp.* are all gymnotiforms, or knifefish [modified from [4]; Srivastava, Szabo (1973); Libouban, Szabo, Ellis (1981)].

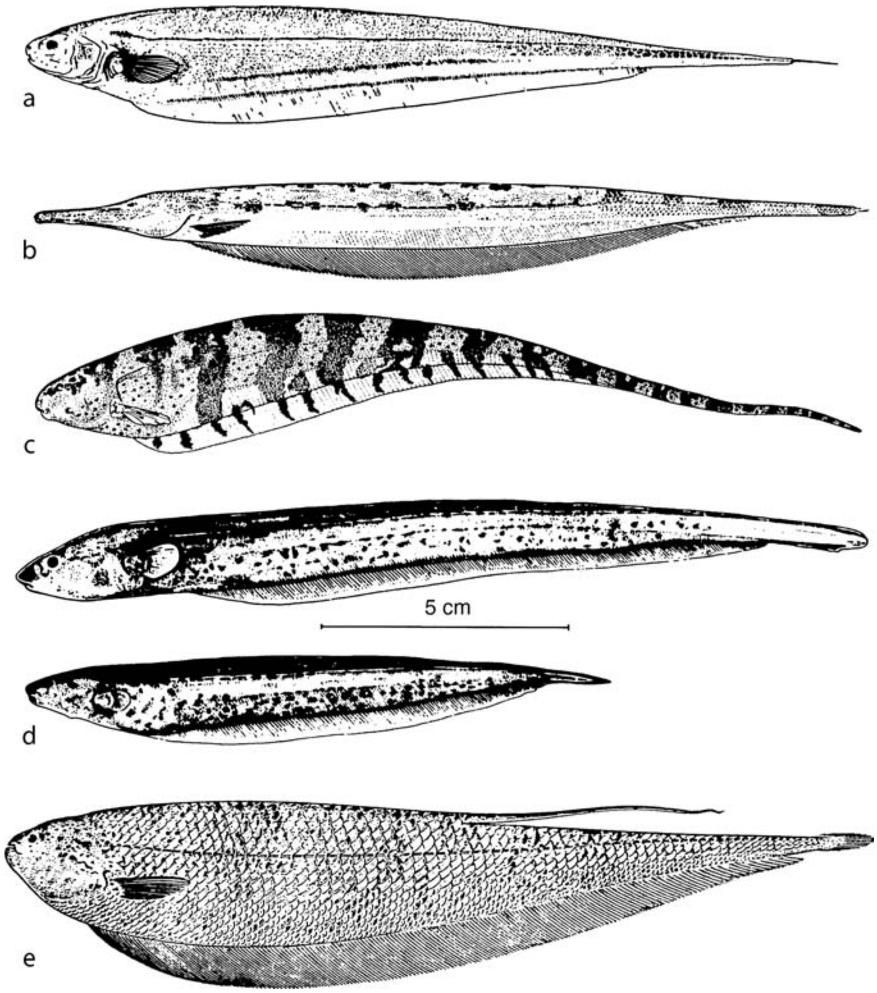


Electric Fish. Figure 2 Several species of snoutfishes (Mormyridae) from the Sudanian ichthyological province, including West Africa. (a) *Hyperopisus bebe*. (b) *Mormyrus rume*. (c) Head of *Mormyrus hasselquistii*. (d) *Campylomormyrus tamandua*. (e) *Mormyrops deliciosus*. (f) *Marcusenius cyprinoides* [Daget, Durand (1981), modified].

the South American knifefishes that are all weakly electric except the electric eel with its powerful discharge (perhaps 150 species; Fig. 3); and the Siluriformes or catfishes, only very few, exclusively African members of which are electrogenic (including both strong and – less well confirmed – weak electric representatives).

Electric organs have evolved at least six times independently of each other: two times among the rays, and four times among the teleosts.

By independent evolution, electric organs are a derived group character for both Mormyriformes and Gymnotiformes, that is, present in all members of their group, but not in their respective sister groups (a synapomorphy). Perhaps a similar situation applies for the skates and the electric rays. This is in contrast to the large taxa catfish and perches, only very few members of which are known to posses electric organs. For a taxonomy of Mormyriformes, see [6]; Gymnotiformes, [7]; constantly up-dated is The Catalog of



Electric Fish. Figure 3 Several species of knifefishes (Gymnotiforms). (a) *Eigenmannia sp*. (b) the sandfish *Gymnorhamphichthys hypostomus*. (c) *Steatogenys elegans*. (d) Male (longer size) and female *Hypopomus occidentalis*. (e) *Adontosternarchus balaenops* ([3], after several authors).

Fishes, online at http://www.calacademy.org/research/ichthyology/catalog/fishcatsearch.html.

Phenotypes

The terms strongly and weakly electric fish delineate alternative adaptations and behavioral strategies, or phenotypes, but do not correspond to phylogenetic categories; there is even one species, the South American electric eel, *Electrophorus electricus*, which is both strongly and weakly electric. “Strong” electric organs are discharged in pulse volleys for brief periods of time only, while attacking prey or during defense; these discharge volleys cause discomfort or pain to a human handling a fish [4]. A particularly strong discharge is that of an attacking or disturbed electric eel which is, according to historical notes from South American natives, capable of “knocking a man down” in its natural environment.

Weak electric organs operate continuously throughout life, and field intensities are usually below detection threshold for non-electroreceptive organisms. Weak electric organs form part of an information system, communication and active electrolocation (see entry “►electric communication and electrolocation”). There are a few intermediate cases, such as the stargazers, whose predatory attack is accompanied by discharge volleys, even though the discharges are much weaker than usual in strongly electric fish; on the other hand, the discharges of *Mormyrus hasselquistii* are unusually strong for a snoutfish, all weakly electric, and can also cause mild discomfort to a human handling this fish.

Among weakly electric, teleost freshwater fish, the Mormyriformes and Gymnotiformes, there are two phenotypes of EOD, wave and pulse, both of which encode social signals as discharge rate modulations.

The pulse EODs of very few species resemble the monopolar time course or waveform of strong discharges; in most weakly electric pulse fish, EOD waveform is bipolar with two or more phases (reducing energy in the low-frequency range of the amplitude spectrum). The wave EODs of wave species are relatively broad pulses that are repeated at such a high and regular rate that they merge into a continuous A.C. wave. While a pulse fish, although discharging continuously, is silent most of the time (because the duration of an EOD is short compared to the inter-EOD interval), a wave fish's signal is always "on" (except on rare occasions, a brief "off" being a display of social significance).

While in Africa the wave discharge type is represented by a single species, *Gymnarchus niloticus*, the only living member of the Gymnarchidae (which is the sister family of the Mormyridae), there are two families of wave fishes in South America, the Sternopygidae, and the still larger family of Apteronotidae (with their neurogenic electric organs). In contrast to Africa, in South America wave species are far more numerous than pulse species.

We are still unable to identify the selection pressures that shaped the ancestors of certain Mormyriformes and Gymnotiformes to discharge their organs either in pulse or in waveform, with only one living species known to date that may represent a transitional state (Fig. 3.18 in [3]). Wave and pulse fishes are found on both continents that are home to the Mormyriformes in Africa, and the Gymnotiformes in South America. The intricate pattern of speciation in the tropics, leading to the highest degree of biodiversity on earth, is a subject of prime interest for which weakly electric fish have proven to be particularly amenable (e.g. [8]).

In contrast to the monopolar EODs of strong-electric fish, the EODs of many weakly electric pulse and (as far as we know) all wave species lack energy in the D.C. and low-frequency range. This seems to be an adaptation to electroreceptive catfish, some of which are voracious, piscivorous predators (see entry "►electric communication and electrolocation"). Catfish are sensitive to low-frequency electric fields by their small pit organs (that are functionally equivalent to ampullary electroreceptor organs and often referred to by that name).

Embryology of Electric Organs

Electric organs usually form from modified muscle cells, or electrocytes, which are unable to contract but are still capable of generating action potentials that are often unusually large [9]. In different species, electric organs are derived from the most diverse muscles and thus can be found almost anywhere in a fish's body. For example, in the mainly marine skates, the organs are located in a slender tail filament, while the strong electric organs of rays form part of the head region of their flattened, disc-shaped bodies ("pectoral" position; Fig. 1).

In the snoutfishes (Mormyriformes), two possible locations of electric organs are found: (i) a rather long and massive electric organ located posteriorly in the body trunk that arises from several columns of axial muscle (up to a third of a fish's length). This has been established in larval specimens for a few species of the family Mormyridae, and such a larval organ grows into the adult organ in the only representative of the Gymnarchidae, *Gymnarchus niloticus.* (ii) In the mormyrid species studied so far, the larval organ starts to degenerate when about 50 days old; while a compact adult organ starts to operate (simultaneous operation of the two organs for a short transition period). The adult organ is located more posteriorly in the caudal peduncle of the tail fin [10].

In the strongly electric catfish *Malapterurus electricus* from African freshwater bodies (the best-known among several, only recently discovered, new species), the electric organ forms from peripheral muscle cells (apparently pectoral), enclosing the body as a tight jacket. In a few members of small catfish, the squeakers (Mochokidae), an organ located dorsal to the swim bladder that may have formed from sonic muscles has been reported to generate very weak and irregular electricity.

In most South American knifefishes (Gymnotiformes), the electric organ forms from several columns of axial muscle. The organ is very long, running from the tip of the tail to near the pectoral fins. Many gymnotiforms have accessory electric organs, the function of which is unclear. In one gymnotiform family, the Apteronotidae, the electric organ forms from presynaptic endings of spinal motor nerves, even though larvae form a temporary organ of myogenic origin that degenerates early in life.

The dipole fields generated by electric organs are usually horizontally orientated, in a fish's long axis; so is the orientation of the electric organ. In a few cases, however, the field vector (that is, current flow) is vertically orientated; the same holds true for these fishes' electric organs. In the strongly electric rays and the stargazers, this is in agreement with these fishes' vertically directed prey capture behavior.

Impedance Matching

Electric organs consist of closely packed, orderly arranged groups of cells, electrocytes, with each electrocyte innervated separately by a spinal electromotor neuron. As the whole organ is enclosed by a tight jacket of connective tissue, there are only little shunt currents, and the voltage differences generated by the individual electrocytes add up (like in a serial arrangement of batteries). The electric current generated by the organ is channeled such that it must leave the body in order to return to the opposite pole of the source. This is important in freshwater fish with water conductivity far below the conductivity of body fluids (usually below 100 μS/cm for tropical freshwaters vs. 5,000 μS/cm for body fluids, or, in resistivity terms, 10 kOhm × cm vs. 200 Ohm × cm, respectively) [4].

In strongly electric fish, impedance matching to the surrounding water is especially obvious, both on a gross morphological level and also regarding membrane physiology. In freshwater fish, such as the South American strongly electric eel, there are only about 70 columns arranged in parallel, consisting of about 6,000 electrocytes each. Therefore, in this fish, it is the voltage that is maximized (500 V or more). In a marine environment, this would not be possible; here, it is the current that should be maximized. Accordingly, in the strong electric rays, such as the *Torpedo* species, there are many relatively short columns arranged in parallel, yielding a low-voltage strong-current output. The number of columns is 500–1,000, the number of electrocytes per column about 1,000. The discharge amplitude is only 50 V in air, corresponding to a massive power output of greater than 1 kW at the peak of the pulse. For an unknown reason, marine electric fish generate (unusually large) postsynaptic potentials (PSPs) rather than muscle action potentials.

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Electric Organ

Definition

So far only electric fishes are known to possess electric organs. In most cases myogenic organs generate electric fields. Some fishes, like the electric eel, use strong fields for prey catching or to ward off predators, while others use weak fields for electrolocation and communication.

Specialized organs in electrosensitive fishes – mostly derived from muscle tissue – that give off electrical discharges, both pulse-like and sinusoidal, under the control of the nervous system.

►Electric Senses in Monotremes: Electroreception and Electrolocation in the Platypus and the Echidna
►Electrolocation
►Electroreceptor Organs
►Reafferent Control in Electric Communication
►Temporal Coding in Electroreception

Electric Organ Discharge

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Synonyms

EOD; organ discharge

Definition

Certain fish possess an electric organ that, on brain command, generates a three-dimensional electric dipole field around their bodies. Compared to incidental stray fields as measured close to any organism [1], an electric organ discharge (EOD) is characterized by a stronger amplitude, higher temporal and spatial stability, and a