# ON THE FUNCTION AND EVOLUTION OF ELECTRIC ORGANS IN FISH

By H. W. LISSMANN
*Department of Zoology, Cambridge*

(With Plates 5 and 6)

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## I. INTRODUCTION

The inadequacy of functional and evolutionary theories of electric organs in fish has been apparent for a long time. Fish are the only class in the whole animal kingdom known to possess specific electric organs. This fact appears noteworthy because (i) the material from which these organs are derived, muscular tissue, is commonly present in other groups of animals; (ii) in fish these organs must have evolved several times independently. This latter conclusion is based first on the occurrence of electric organs in widely unrelated families, and secondly on the fact that electric organs are developed from different parts of the body.

Although it is frequently stated that electric organs are remarkable adaptations, e.g. in having the electric elements suitably arranged in parallel or in series to conform to the conductivity of either fresh or sea water, very little has been known until recently of the biological significance of these organs—apart from a subjectively experienced defensive action and a surmized offensive role. This is probably the main reason why the problem of their evolutionary history, clearly stated by Darwin (1872), still awaits a satisfactory answer. Dahlgren (1910), after a detailed examination of 'the origin of the electricity tissues in fishes', comes to the conclusion 'that the impulse to evolve this tissue is a real inner stimulus working independently of outer conditions....The evolution of these structures was most probably not based upon a basis of natural selection.'

It has been customary to distinguish between strong electric organs and pseudo or weak electric organs. Most workers in recent years have been concerned with physiological aspects of electric tissue, and have availed themselves mainly of *Torpedo* and *Electrophorus*, both fish giving off strong electric discharges. It appears that an investigation of the weak electric fishes is more likely to reveal possible evolutionary starting points. Apart from the fact, established towards the end of last century, that the weak electric organs are capable of giving off weak electric discharges (Babuchin, 1877; Sanderson & Gotch, 1888; Fritsch, 1891) very little new information has come to light, and the functional significance and evolutionary history of the weak electric organs have remained obscure. Suggestions, which have been put forward in the past, about the role and mode of action of weak electric organs appear implausible; e.g. that weak electric fish, feeding on insect larvae, worms and crustacea may be able to stun their small prey before swallowing it; or that weak electric fish were simulating strong electric fish, thereby deriving a certain amount of protection.

As has been reported previously (Lissmann, 1951) a specimen of *Gymnarchus niloticus* aroused interest through its navigational abilities. This fish, which frequently swims backwards, appears to avoid obstacles, to find its way through crevices in rocks, and to locate its prey from a surprising distance. This makes it unlikely that either the poorly developed eyes, or any conventional concepts of perception of water currents or water pressure through the lateral line, could account for such a performance. Structurally the species *G. niloticus* has been known to possess small organs, assumed to be electric (Erdl, 1846), although this had not been generally accepted (Fritsch, 1885). Preliminary experiments indicated that these organs were indeed electric, and they appeared to play an important role in the orientation of *Gymnarchus* and also of two other species of teleost fishes. The theory then suggested for this mechanism implied that fish may be able to detect objects at some distance by appreciating their electrical conductivity which can be expected to differ from that of the surrounding water (Lissmann, 1951). It was, therefore, decided to obtain additional information and to investigate these species in their natural habitat in West Africa as well as in the laboratory.

However, working conditions in the field and scarcity of living material in the laboratory have imposed serious limitations on the nature of experiments which could be undertaken hitherto. It cannot be claimed that the observations reported here have reached any degree of completeness; nevertheless, they clarify the picture to a certain extent, and this investigation is being continued as more material becomes available.

The problems of electric organs, which will be dealt with in this and subsequent papers, are mainly concerned with (i) their possible use as part of an orientating mechanism; (ii) the mode of action of this mechanism; (iii) its biological significance. It is hoped that some lines of evolution of the electric organs may thus be revealed.

In this inquiry it seems important that the electric organs should be considered not just as organs interesting in themselves, but rather as a part of the general bodily organization of the fish, having a role to play in the relation between the fish and its environment.

## II. MATERIAL AND PROCEDURE

Most of the material used in the present study was collected in 1951 in the course of an expedition to the Northern Territories of Ghana. The fish were caught in the Black Volta and its tributaries Kamba, Sielo, Poni, etc.; some additional species were obtained from other parts of Africa and from South America.

It was noted that the water of the natural habitat of the fish under discussion was extremely turbid in the dry season (February to May); the particles in suspension appear to be very fine as it takes several days before the water, kept stagnant in an aquarium, becomes reasonably clear. During the rainy season, with increasing soil erosion, turbidity becomes even more marked. Under such conditions the eyes of the fish would appear of little use and this may be expected to favour the evolution of alternative sensory mechanisms.

The presence of electric fish in any particular stretch of river or in drying-up pools could be detected by a pair of electrodes suspended from a boat or from a pole on the bank. The electrodes, copper wire 1 cm. long and 12 cm. apart, were connected to a battery-driven three-stage amplifier and electric pulses were noted either by the use of headphones, or by visualization on a G.E.C. Miniscope (6 V. d.c. using a vibrator). On many occasions it was found possible to hear the discharges, though more faintly, by connecting the headphones directly to the electrodes without any amplification; headphones of 16 and 2000 Ω proved equally suitable. At a later stage pulses observed in rivers and pools were registered for further examination by means of a magnetic tape recorder.

These observations revealed a number of different types of discharges, best seen in the main rivers, where an absence of crowding makes analysis easier. Rhythmic or regular recurrence of similar spikes was taken to mean a single source of emission. Broadly, the types of discharges can be placed in the following categories:

(1) On five separate occasions (Black Volta, Kamba, Sielo) a very uniform hum of approximately 300 cyc./sec. was heard. Although in one instance these very regular pulses were seen on the oscilloscope, it was at that time not possible to make a recording. The spikes were monophasic; the duration of each spike seemed to extend over a few milliseconds. Thus, they clearly resembled the previously noted discharges of *Gymnarchus niloticus*.

(2) Fairly regularly spaced and constant pulses, varying in frequency between 1 and 6/sec., were heard and recorded on frequent occasions. When the electrodes were left in the same position in the water the size of the spikes remained constant for long periods. It was assumed that this indicated relatively stationary specimens (Pl. 5, 1*a*). Sometimes it also happened that the frequency of such pulses—apparently emitted by single specimens—showed periodic variations in frequency (Pl. 5, 1*b*). Whenever a heavy stone was thrown into the river, or a pole thrust in the general direction of the electrodes, the pulses usually quickened and disappeared for good. However, it was also noted on several occasions that when the bottom of the boat was tapped or thumped the pulses disappeared abruptly for a few seconds to reappear with their previous characteristics. All these pulses were polyphasic and each pulse appeared to be of very brief duration, i.e. less than 1 msec. and, therefore, difficult to record photographically in the field in any detail. These discharges appeared similar in frequency and shape to those observed in *Mormyrops boulengeri* (Lissmann, 1951).

(3) Similar pulses of higher frequency, usually between 20 to 50/sec., were also observed and recorded on many occasions without any deliberate disturbance having been caused. Normally such pulses, which could be attributed to a single source, remained in evidence only for a short period of time, i.e. presumably the fish were swimming past the electrodes (Pl. 5, 1*c*). However, in small drying-up pools, where there was a high concentration of fish, electric signals could be picked up almost continuously (Pl. 5, 2).

(4) Only on one occasion four short, but distinct bursts were picked up and heard in the Black Volta; the estimated frequency was about 120/sec.; the duration of each burst was probably of the order of 1 sec. The frequency was appreciably higher than that of *Gymnotus carapo* which had been examined earlier in the laboratory (Lissmann, 1951) and which has a normal frequency of about 50 pulses/sec.

(5) On a number of different days when the headphones were directly connected to the electrodes, and the latter lowered close to a rock into the Black Volta (near Buga), an extremely powerful and brief discharge, consisting of a train of pulses, could be evoked repeatedly. Since the strength of the discharge appeared of an entirely different magnitude from those discussed above, it was ascribed to *Malapterurus electricus*, the only strong electric fish known to exist in that area.

For further investigation in the laboratory attempts were then made to catch the fish which emitted these discharges. In most localities in the rivers it was possible to use cast nets only; in smaller pools a miniature seine net was used with success, and practically all fish could be taken from such pools. On two occasions I benefited from the visit of the Fisheries Officer who operated a large seine net with local fishermen, and this made it possible to extend the collection.

Fish were kept in large, round native clay pots (80 cm. in diameter); although the water evaporated at a considerable rate and had to be replaced at frequent intervals, it remained much cooler than in other containers and the fish survived well. During catching expeditions kerosine tins were found to be useful and manageable receptacles for transport of the smaller species. For observation and experiments a collapsible aquarium (66 × 33 × 35 cm.) was constructed of rubber-edged Perspex plates which were clamped into a metal frame; two large accumulator jars could also be used for the smaller species. Aeration was provided by diffusing air from an R.A.F. oxygen cylinder which had to be pumped up twice daily by means of a car tyre pump to a pressure of between 40 and 50 lb. Some of the fish were taken to the Department of Zoology, Achimota, for examination and later brought back to Cambridge, and are still alive at the time of writing.

## III. *GYMNARCHUS NILOTICUS*

The pulses mentioned under (1) in the previous section were clearly identical with the signals already described (Lissmann, 1951) which are produced by the species *Gymnarchus niloticus*. The characteristics of these discharges are quite distinct from any produced by other species of fish in that area. Unfortunately, specimens were not as abundant as had been expected from records of catches made by Dr K. R. S. Morris at the same localities in previous years. A number of these fish were observed coming to the surface, often near fallen trees in the rivers, where capture appeared impracticable. In all, nine specimens were obtained; some of these were too large to be kept alive for any length of time. In addition to the first fish, 28 cm. in length, observed for 7 months in Cambridge, two more specimens were eventually brought back for further study: they now measure 52 and 54 cm. respectively.

*Gymnarchus* is a predator which feeds on other fish, and it can attain a considerable length. Svensson (1933) records a specimen of 160 cm. This species has been noted from various parts of East and West Africa north of the equator. The genus is monospecific and represents one of the two suborders of the Mormyriformes, the other being the Mormyroidei (Berg, 1947). Other authorities include this fish as a separate genus amongst the Mormyridae.

Apart from a similar geographical distribution *Gymnarchus* shares with the Mormyroidei a number of anatomical peculiarities, e.g. a vesicle of the swimbladder is applied to the inner ear, it has enlarged valvulae cerebelli, an opercular velum, a caudal electric organ, etc. On the other hand, *Gymnarchus* differs from the Mormyroidei in many striking features: the elongated body is without tail fin, anal fin or pelvic fins, but the fish possesses a very long dorsal fin; the swimbladder is adapted for atmospheric respiration and the circulatory system is accordingly modified; the electric organs are substantially different from those of the Mormyroidea. For further details of the anatomy and development of *Gymnarchus* reference must be made to the publications of Erdl (1947); Hyrtl (1856); Fritsch (1885); Ridewood (1904); Asheton (1907); Dahlgren (1914); Stendell (1914*a*); Pehrson (1945); Omarkhan (1949).

We owe to Budgett (1901) the first detailed field observations of this fish and also a description of its breeding habits. *Gymnarchus* builds a nest of floating vegetation in the middle of which there is a 'private pond'; into this are laid eggs, measuring 1 cm. in diameter. The parent fish keeps guard near the nest and is, apparently, very aggressive. The material of eggs and embryos collected by Budgett forms the basis of much of the subsequent anatomical and embryological work on this species.

The specimens available for the present study measured between 28 and 85 cm. In the laboratory they were kept in electrically heated aquaria at temperatures between 25–30° C. The largest experimental tank measured 120 × 75 × 45 cm. The food consisted mostly of minnows and gudgeons. *Gymnarchus* displays considerable agility in locating and catching its prey; this often appears to be sucked in by an expansion of the branchial basket and is accompanied by a resounding snap. Larger fish are often bitten in half before being swallowed. *Gymnarchus* shows marked cannibalistic tendencies; individuals have therefore to be kept in separate containers. The fish come periodically to the surface for respiration; as the snout breaks the surface of the water a marked longitudinal depression can be observed to form on the ventral side.

Erdl (1846) and Fritsch (1885) have described the electric organ of adult specimens, Fritsch suggesting that it may have some respiratory significance. Dahlgren (1914) has followed the development of this organ up to the 42-day-old embryo. It consists of four 'tube-like' cylindrical structures ('spindles') on either side, extending from the tip of the pointed tail to varying anterior levels. A cross-section through the tail reveals that it is largely made up of these electric spindles; further forward they are closely applied to the median parts of the body. The dorsal and ventral spindles are considerably shorter than the upper median and lower median spindle. Fritsch has found the last traces of the upper median spindle at the level of the pectoral fins: the ventral spindle terminates at the level of the anus. Counts of electroplates composing these organs have been made by Erdl (1846) and by Fritsch (1885) and are given below

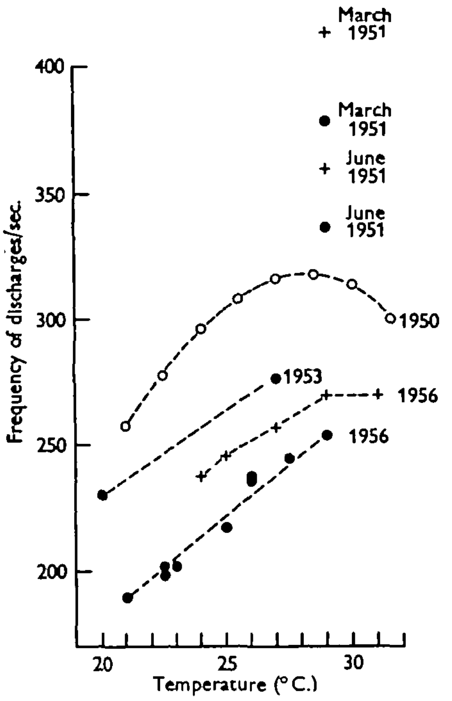
| | Erdl | Fritsch |
|---|---|---|
| Dorsal spindle | 56 | 99 |
| Upper median spindle | 136 | 139 |
| Lower median spindle | 96 | 111 |
| Ventral spindle | 56 | 99 |

Along the middle of its course the diameter of a transverse section of a spindle is stated to be 4·2 mm.; this diameter decreases both anteriorly and posteriorly. These figures are for a specimen 89 cm. in length. The maximal length of an electroplate is given as 1·2 cm. According to Dahlgren (1914) the electric tissue of *Gymnarchus* is developed by the differentiation of striated muscle tissue during the embryonic or larval period from the ninth to the forty-second day. Each electroplate is made up of twelve to twenty or more muscle cells, and receives its nerve supply at the posterior face. The nerves take their origin in large cells situated in the spinal cord dorsally to the central canal, and they emerge through the ventral roots forming four longitudinal electric nerves. In captivity these fish frequently lost and regenerated the last 5–7 cm. of the pointed tail. One specimen in particular often regenerated malformations in the shape of hooks or forks; these, however, were again lost after a few weeks and the perfect, pointed tail reappeared. It has never been ascertained how the damage was incurred as there were no sharp objects in the tank. Only on one occasion, when the tail was nearly broken off and trailing, did the animal turn into a circle and viciously attack its own hind end. This strong curvature of the long body axis is not one of the typical movements of *Gymnarchus*, which may seem surprising in a fish of such elongated shape. One of the most immediately striking features of *Gymnarchus* is its locomotory performance: in all phases of the locomotory cycle the body can be kept predominantly straight. As this type of movement has probably some bearing on the electric locating mechanism (see below), it has been examined in some detail and will be reported in a separate paper.

All specimens, when first examined, emitted an uninterrupted sequence of electric pulses at the rate of approximately 300/sec. These pulses can be displayed either with the fish out of water, by placing two electrodes on the surface of the skin, or with the fish in an aquarium by introducing the pair of electrodes into the water. The observations were extended for many hours under varying conditions; neither intense illumination nor complete darkness seemed to alter the frequency of the discharges, nor did the frequency change when a fish, which had been motionless for some time, was suddenly and vigorously stimulated, nor when a starved fish had been given an abundance of food. However, slight but constant differences in frequency were noted between individuals of comparable size under identical conditions. It has not been possible to relate these differences to sex or any other features.

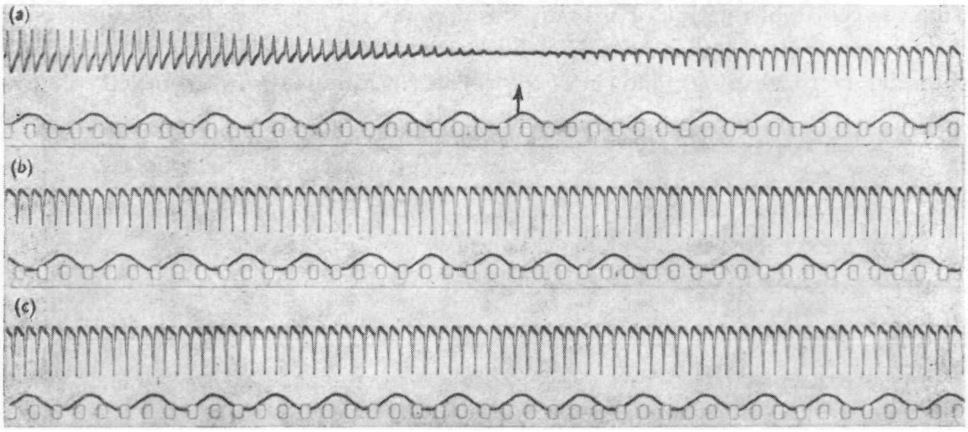
One condition which does affect the frequency in a regular manner is temperature (Text-fig. 1). The temperature of the water observed by Budgett (1901) in the breeding season was 28·5° C., which may perhaps be taken as optimal. Whether diurnal or seasonal variations occur has not been investigated, but a gradual decrease in frequency has been noted in the two specimens which have now been in captivity for over 6 years. In the course of this period the frequency has dropped from about 400/sec. to approximately 280/sec. under comparable temperature conditions (Text-fig. 1). At this stage it is impossible to decide whether this change is related to age, conditions of captivity, or some other factor. No records are available of the largest specimen (85 cm.) as it was too large to be accommodated in an aquarium, but when this fish was examined immediately after capture, lying on dry land, no significant difference was noted in its frequency, compared with that of the smaller specimens. Nor could any shocks be felt by placing wet fingers on its tail and other parts of the body.

As long as *Gymnarchus* is motionless the strength of the individual pulses is remarkably regular and can be easily recorded (Text-fig. 2*b*, *c*). While the fish is swimming or chasing its prey there is no evidence that the voltage alters to any marked extent, but owing to the high attenuation of water and the changing relative position between the fish and the recording electrodes, this is not easily demonstrable with any degree of accuracy. Attempts to determine the voltage of the discharges, with the fish superficially dried and lying on cotton wool, were made on three specimens, by holding one electrode (copper wire) near the tip of the tail and the other about one-third of the body length behind the snout. These fish, measuring 38, 42 and 52 cm., gave each over a period of about 5 min., fairly constant readings of 3, 7 and 4 V., respectively.



Text-fig. 1. Variations in the frequency of impulses exhibited by three specimens of *Gymnarchus niloticus*. Specimen 1 (○) 28 cm. long; note the change in the frequency in the course of a gradual temperature increase within 10 hr. Specimen 2 (+) and 3 (●); note the decrease in the frequency of discharges from the first record (soon after capture) when the fish measured about 38 cm. up to 5 years later when they measured 52 and 54 cm.

That changes in voltage do occur has been noted on the few rare occasions (six in three specimens) when for a brief period the fish failed to emit pulses, after which pulses slowly reappeared with their normal frequency but with gradually increasing intensity. Although this phenomenon of suppression of electric discharges is not reproducible at will, two possible explanations can be offered. In the smallest specimen (28 cm.) it occurred several times when the fish had been caught after a chase and transported from its aquarium to an experimental tank.* The original explanation that the transport in a small metal container was responsible for the disappearance of the discharges proved fallacious. *Gymnarchus* kept for many days in a kerosene tin continued to discharge, and the discharges even continued in moribund specimens after all motility had ceased. Another possible explanation may be suggested based on two similar observations. The clearest instance occurred in Achimota, when two specimens of *Gymnarchus*, kept in separate tanks, had been given an ample supply of food in the course of an afternoon. At 11.30 p.m. the amplifiers were switched on with a minimum amount of noise and in almost complete darkness. One of the specimens appeared normal in the emission of its electrical discharges, while the other over a period of 5 min. did not show any signs of electrical activity. A dim light revealed that the animal was resting on the bottom, but when touched with a glass rod it began to swim still without emitting any electric pulses. The lights were then switched on and both fish appeared to swim about normally without any change in the electrical behaviour. After 1 min. the non-emitting fish was vigorously prodded with a glass rod; 30 sec. later very faint pulses of approximately normal frequency appeared. They gradually increased, until after about 2 min. the signal strength of both fish was approximately equal. It may be implied that the condition of such specimens may be akin to a state of sleep, although this does not seem to occur very often and only one further similar instance has been recorded despite extended efforts.



Text-fig. 2. Continuous record of the electric discharges of *Gymnarchus niloticus* at 23° C. The electrodes, first held close to the posterior end of fish and parallel to its long axis, were rotated by 180° (*a*) and then held stationary (*b*) and (*c*). At ↑ they were pointing to the posterior margin of the dorsal fin. During the discharge the tail becomes negative relative to the more anterior regions of the body. Time marker 50 cyc./sec.

When the recording electrodes are placed in the water so that their distance apart is greater than the total length of a *Gymnarchus*, it will be seen that the train of

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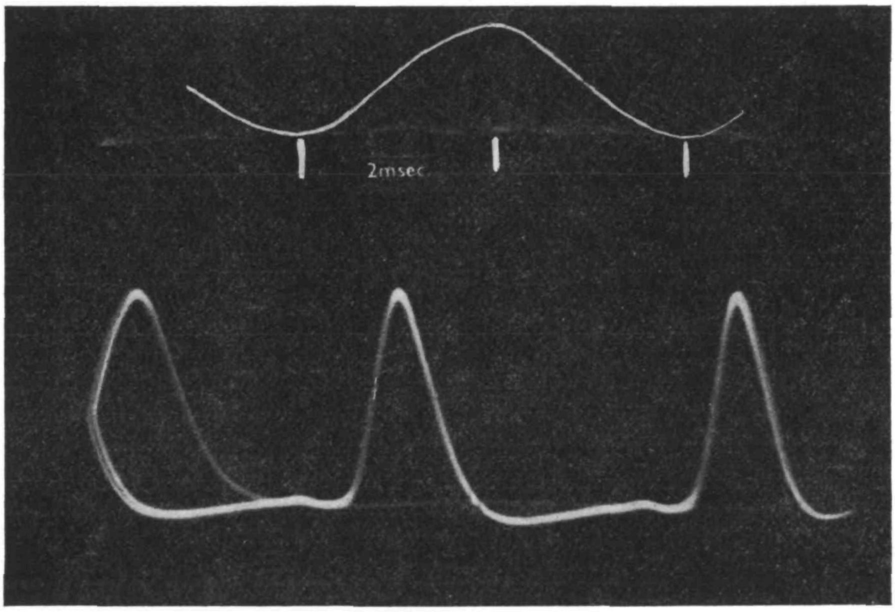
* Analogous behaviour was shown by small specimens of *Gymnotus carapo* during class experiments; they ceased to discharge after inexpert handling.

discharges emitted by these fish consists of individual pulses 1·3 msec. in duration, followed by an interval of about 2·3 msec. (Text-fig. 3). During each discharge the tail becomes negative relative to the more anterior regions. This is in agreement with the Pacinian rule, since Dahlgren (1914) has shown that the innervated face of each electroplate is situated posteriorly.

The shape of the electric field, set up around the fish during each discharge, has been examined by placing a specimen in a large shallow porcelain tank and introducing two recording electrodes (8 cm. apart) which were mounted equidistant from the centre of rotation of a disk. A long pointer attached to the disk indicated the orientation of the electrodes. The alignment of the electrodes on lines of equipotential (zero reading) and lines of force (maximum) was recorded photographically, together with the position of the fish in the tank. This showed that the line of equipotential normal to the long axis of the fish lies near the posterior level of the dorsal fin (Text-fig. 2*a*). Around this transverse axis, however, the field is not symmetrical, i.e. it is not strictly that of a dipole. This can be demonstrated most easily by placing two electrodes close together (2 cm.) and in line with the long axis of the fish. Movement of the electrodes parallel to this axis will show a maximum at the posterior level of the dorsal fin. Displacement of the electrodes from this position in a posterior direction shows a considerably more rapid decrease of the spikes per distance unit of movement, as compared with anterior displacement. This agrees with the anatomical finding, namely, that whereas all electric spindles terminate at the tip of the tail, they extend to varying anterior levels.



Text-fig. 3. Individual pulses of *Gymnarchus niloticus* 27 cm. long recorded at 28° C. The duration of the individual pulse is about 1·3 msec., followed after about 2·3 msec. by the next discharge. Time marker 2 msec.

The suggestion that *Gymnarchus* uses the electric discharges as part of a locating mechanism seemed to be supported by a number of preliminary observations, which indicate that the fish is indeed very sensitive to any influences which may affect the electric field set up with each discharge.

(1) The tips of a wire loop, interrupted by a switch, were dipped some 2 mm. into the aquarium water. Normally, unless the fish came very close to the wires, it took no notice. However, when it swam past the wires and the switch was suddenly closed, the fish performed a violent jerk. While this may suggest that the normal configuration of the electric field was upset in this experiment through the outside circuit, it is realized that metals in contact with water will generate on their surfaces electric currents to which a fish may respond (Parker & van Heusen, 1917). Until more quantitative information about the sensitivity of *Gymnarchus* is available, it seems premature to draw any final conclusions from this observation.

(2) It is very obvious that *Gymnarchus* will respond to the presence of metals in the water, although if the metal is left long enough in an aquarium the fish seem to get habituated and shows no behavioural responses. One striking type of behaviour was shown by a small specimen when four straight pieces of bare copper wire, about 50 cm. long, were placed on the bottom of a shallow tank to form a rectangle. When the fish was placed inside this rectangle it appeared trapped within it. Every time it approached a wire, it shied and reversed. When the fish was eventually chased, it slipped over the wire as near as possible to the surface of the water and lying on its side.

(3) The cannibalistic tendencies of *Gymnarchus* have already been mentioned. It appears that two specimens can detect each other's presence at some considerable distance. In order to examine whether or not the emission and perception of electric pulses plays an important role in this, a large shallow tank was filled with water to a depth of about 12 cm. In the middle of this tank a pair of receiving electrodes was fixed to pick up the impulses emitted by the fish. These impulses were then amplified to about 3 V. and continuously adjusted to approximately that value as the fish was swimming about. Round the edges of the tank six pairs of electrodes were immersed and could be successively connected to the output of the amplifier. The fish quite clearly located and attacked whichever pair of electrodes emitted the signals. Within a wide range the frequency of the signals does not appear essential, since the fish behaved similarly to signals of frequencies other than its own, which were fed into the tank by means of a beat-frequency oscillator. This experiment may indicate the general anti-social tendencies in *Gymnarchus*, but it may be expected that under certain circumstances, e.g. in the breeding season, these tendencies are not indiscriminate. No information is available on this point. A study of electrical and other behaviour responses of a breeding pair may be most rewarding.

(4) It was clearly of interest to obtain an indication of the fishes' sensitivity to electrical changes—which must be considerable if the suggested hypothesis is to work—without any direct contact between metal and the water of the aquarium. Two examples may be selected to illustrate the degree of sensitivity of *Gymnarchus*.

(i) The fish shows marked responses to the movement of a rod magnet of a dipole moment of about $5 \times 10^5$ e.m.u. operated at some distance behind a screen. At shorter range, *Gymnarchus* can be pulled along, as it were, and reversed by a magnet which is slowly displaced along the slate wall of its aquarium. The fish has also been trained to avoid its feeding place and food when a stationary magnet was placed near it (not visible), and to accept the food when the magnet was removed, and vice versa. Comparable experiments with minnows (*Phoxinus phoxinus*) have, so far, produced no positive results, although these fish could be trained to optical stimuli within 2 days.

(ii) Similarly, *Gymnarchus* has been found to respond to the movement of a small electrostatic charge, such as is produced by combing one's hair with a vulcanite comb.

A more quantitative treatment of this aspect, combined with conditioned reflex experiments will be given in another paper (Lissmann & Machin, 1958).

## IV. MORMYRIDAE

Most, if not all the electric discharges mentioned in § II—apart from those of *Gymnarchus* and *Malapterurus*—could be traced to representatives of the family Mormyridae. These are highly aberrant, mostly curious-looking fishes, very variable in the form of body, head and fins (see Text-fig. 5). Boulenger (1909) places them close to the Albulidae or Elopidae and lists ten genera. One or more species of seven of these genera have been examined in the course of the present investigation. These genera include *Mormyrops*, *Petrocephalus*, *Isichthys*, *Marcusenius*, *Mormyrus*, *Gnathonemus* and *Hyperopisus*. Not all the species have yet been identified with any degree of certainty, as the present survey of the electrical behaviour of this family was undertaken mainly in the hope of finding suitable experimental material.

Despite their great diversity in size, form and life habits (Schlesinger, 1909), which will not be discussed here, all representatives share some outstanding structural features. The most noteworthy of these, which probably have some direct bearing on this enquiry are:

(1) The caudal electric organ, first described by Rüppel (1832) as 'two elongated jelly-like masses situated below the tendons of the double-bellied muscles which move the tail fin in a horizontal direction'. In the course of the last century much anatomical and histological work has been done on these organs by Marcusen (1864); Babuchin (1872); Fritsch (1891); Ogneff (1898); Schlichter (1906).* The organ generally extends from the posterior level of the dorsal fin to the tail fin. On either side it is subdivided into a dorsal and a ventral portion, and each of these is composed of 150 to 200 longitudinally arranged electroplates. The nerve supply to this organ emerges from the ventral roots of the spinal nerves in the area of the caudal peduncle. The nerve divides to form a dorsal and a ventral branch of the electric nerve; moreover, there is an interchange of fibres (chiasma) of these peripheral nerves above and below the vertebral column. Babuchin (1877) and Fritsch (1891) have made use of an anuran nerve-muscle preparation to display the

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* Szabo (1957).

discharges of Mormyridae, by placing the nerve on the electric organ of a fish. Babuchin observed hopping movements of a toad's leg up to 5 min., giving four to five twitches per second. While these observations can be confirmed, the limitations of the method became obvious after it was established (Lissmann, 1951) that *Mormyrops boulengeri* could give off discharges of considerably higher frequencies. No modern physiological data on the electric organ of Mormyridae appear to be available.

(2) A pair of styliform, longitudinal bones ('Gemminger's bones') are found above and below the electric organs. No comparable structure is known to occur in any other group of fish. Apart from the statement by Marcusen (1864) that these bones have nothing to do with the pseudo-electric organs, and serve as attachment for some tail muscles, little attention has been paid to this peculiarity.

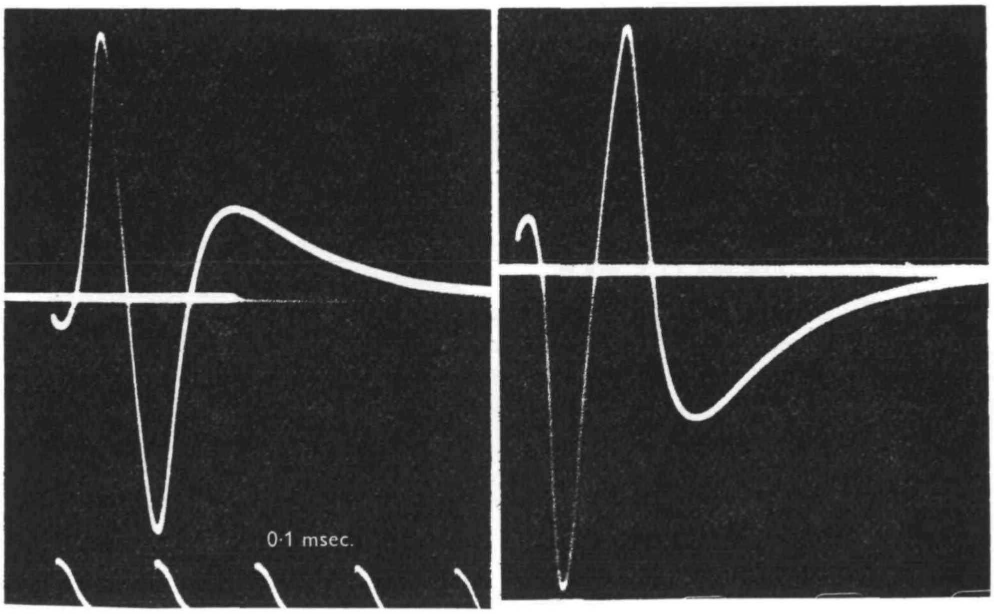
(3) The Mormyridae possess a thick, multi-layered epidermis which extends over the eyes, opercular bones, etc., and it contains small foramina (Marcusen, 1864; Franz, 1921). The basal layer of the epidermis is composed of cylindrical cells; this is followed by three to four layers of polygonal cells. Over this are found regular, more or less hexagonal pillars composed of approximately forty flattened cells. The outermost layer is again formed by three to four rows of polygonal cells. This, as far as is known, is a unique epidermal organization amongst fishes.

(4) The foramina in the epidermis lead through canals to peculiar cutaneous sense organs which have been a point of some controversy (Franz, 1912, 1921; Stendell, 1914*a*, *b*, 1916). The balance of opinion has now definitely shifted in Stendell's favour and these 'mormyromasts' are considered as specializations of lateralis sense organs (Cordier, 1938; Gérard, 1940).

(5) Similarly, the enormous cerebellum ('mormyro-cerebellum') is now considered predominantly as an association centre for this undefined sense (Sanders, 1882; Franz, 1912, 1921; Stendell, 1914*a*, *b*, 1916; Berkelbach van der Sprenkel, 1915; Suzuki, 1932).

The possible relationships of these structures will be discussed later. Here it may be noted that although the Mormyridae are considered to be related to *Gymnarchus*, their electrical discharge characteristics differ substantially from those of that species. The most striking of these differences are the great variation in frequency which any one individual can produce, and the very short duration of each polyphasic pulse (Pl. 6). Although there are some differences in the electrical behaviour of different species of Mormyridae, the similarities of all the examined species are on the whole greater than the differences. While the basic discharge rate of a resting animal is usually somewhere between 1 and 6 pulses/sec., in extreme cases the pulses can either cease altogether for several seconds or minutes, or conversely they can be accelerated up to about 130 discharges/sec.

The conclusions drawn from observations of electric pulses in the rivers, namely, that resting fish discharge at a lower frequency while in active fish or in disturbed fish (which need not perform any movements) the rate of discharges is speeded up, has on the whole been confirmed by examination of fish in aquaria. A representative selection of records is given in Plate 6. These were taken with the various species of fish originally at rest (top record) and then excited either by a tap on the aquarium wall or by touching them with a glass rod (lower record). It must be mentioned, however, that bottom-living forms such as *Isichthys henryi* or *Mormyrops breviceps* were more often found resting motionless on the bottom, as compared with some of the smaller, active mid-water species such as *Petrocephalus* and *Marcusenius*. In consequence, it appears that the discharge rate of the latter, even when not disturbed, was rather higher; but after a disturbance their accelerated pulse rate did not persist so long.



Text-fig. 4. Single pulses from the whole organ of *Petrocephalus* sp. (Sudan) 5 cm. long. Distance of recording electrodes 12 cm.; their position is reversed by 180° in the two records. Time marker 0·1 msec.

Two types of stimuli were encountered: some which accelerated and others that slowed down or completely suppressed the discharges. For example, two specimens of *Mormyrus rume* which discharged in regular fashion inside the laboratory ceased to discharge altogether as soon as their aquarium was placed in bright sunlight. The possibility was therefore considered that these discharges might be of special significance when the eyes were unable to function. However, although it was found that switching off the lights in a darkroom produced an accelerated burst of discharges (*Isichthys henryi*, *Mormyrops breviceps*, *Gnathonemus senegalensis*) which often persisted since the animals became more active, a similar burst was elicited when the lights were again switched on.

A considerable difference in behaviour was also noted between animals which had been kept for a long time and had settled down in aquaria and those that had been recently captured and had spent only a few weeks or months in an aquarium.

Thus, in Africa frequencies above 50 pulses/sec. were rarely recorded from fish in captivity, while the highest frequency observed in a river was at least twice that figure. The reason why the search for a mormyrid of such high discharge frequency was fruitless can probably be explained, because a *Gnathonemus senegalensis* which had been kept in an aquarium for over 6 years (before it perished in an accident) did discharge regularly with frequencies up to 130/sec. when touched with a glass rod (Pl. 6). But this same animal—and others—always ceased to discharge when a person approached the aquarium and leaned over it. These silent periods could last up to 30 sec., occasionally punctuated by a single pulse. Eventually the normal discharges were resumed. Analogous behaviour was also noted in other species, particularly in forms with well-developed eyes. A loud noise would sometimes have the same effect.

Thus, most of the observations made in the natural habitat could be repeated on fish in captivity. The rarely noted grouping of discharges into two pulses followed by a longer interval has also been recorded in a few cases from fish in captivity, notably in some specimens of *Hyperopisus bebe* (Pl. 6), but no explanation can be offered for this type of behaviour.

The measurement of the voltage of these discharges was carried out as in the case of *Gymnarchus*, by placing two electrodes superficially on the fish out of water at the levels of the two ends of the electric organ. The results for *Gnathonemus senegalensis*, *Mormyrus rume*, and *Hyperopisus bebe*, 12–19 cm. long, were somewhat variable. 9 to 17 V. were thus registered, but the differences of individual measurements could not be directly related to size or species of the fish.

When a pair of electrodes is placed in an aquarium with an actively swimming mormyrid it will be seen (i) that the size and shape of the pulses displayed on an oscilloscope vary with the relative position of fish and electrodes; (ii) that when the distance between the electrodes is greater than the total length of the fish the individual pulses are polyphasic and, considering that they are emitted from the whole organ, of extremely short duration (about 0·2 msec. in the case of *Petrocephalus*, Text-fig. 4). This seems to indicate a propagated phenomenon over the electric organ but the details of the discharge mechanism are not understood.

While records from rivers and pools frequently indicated solitary specimens, other records showed aggregations or schools of fish (Pl. 5). This seemed to be in contrast to the behaviour of most species in captivity. Despite their small mouths they appeared to attack each other and the damage inflicted led to many casualties. It was noted that the attacks were often directed towards the tail end. As in the case of *Gymnarchus* it can be assumed that this unsociable attitude shows variations throughout the year.

In order to determine whether, in addition to other functions, the electrical discharges may be of social significance some preliminary experiments were carried out in Africa. A cloth partition was fixed in an aquarium dividing it into two equal halves. This partition consisted of a wooden frame over which the cloth was stretched on both sides, so that the two layers of cloth were about 2 cm apart. This frame was fitted into the aquarium by means of plasticine, and could be expected to be transparent to electrical but not to visual stimuli. One *Gnathonemus senegalensis* was introduced into one compartment of this tank and allowed to settle down for 2 days. After this period a second fish of the same species was carefully introduced into the second compartment. Both fish were resting motionless on the bottom. Recording electrodes introduced into the tank showed that both fish were discharging at a fairly low and regular rate. Whenever one of the two specimens was gently touched with a glass rod its discharge rate went up abruptly and the fish in the other compartment usually followed suit. When one of the fish was removed, a similar movement of the glass rod in the empty compartment remained without effect. These two specimens were left in the tank overnight. After darkness the light of a dim torch showed them both swimming up and down on the opposite sides of the partition, obviously taking note of each other's presence and discharging with higher frequencies. Bursts of discharges from both fish coincided when they came close together, but no correlation in the timing of individual pulses was noted. This observation, though not conclusive, does suggest that the electrical discharges may play a social role in the life of the Mormyridae.*

On the other hand, I have completely failed to note any effect of the discharges on the behaviour of the prey of the Mormyridae; *Daphnia*, *Chironomus* larvae, *Tubifex* and *Enchytraeus* appeared equally unaffected.

## V. GYMNOTIDAE

The family Gymnotidae is considered to be an offshoot of the Characidae (Boulenger, 1904). Thus, according to the generally accepted characters, they are not assumed to be of close relationship to the Mormyridae. Although some anatomical and histological information about the Gymnotidae is available, it is largely restricted to *Electrophorus electricus*, and is more scanty than comparable information of the Mormyridae. Nevertheless, a great many structural and functional similarities are found in both these families (Text-fig. 5). Of particular interest is the mode of locomotion which is closely analogous to that of *Gymnarchus*, except that in this instance the long anal fin acts as propulsive organ.

Systematists have separated *Electrophorus electricus* from the rest of this group as being an 'electric fish' (Regan, 1911; Ellis, 1913), although structurally similar electric organs have been described in other genera or subfamilies (Ellis, 1913; Lowrey, 1914; Schaffer, 1917). Since the fact that *Gymnotus carapo* gives off weak electric discharges was reported (Lissmann, 1951) a number of other gymnotids have been described as electrogenic (Coates, 1955; Couceiro, Leao & Castro, 1955; Grundfest, 1957), and it may reasonably be assumed that, like the Mormyridae, all Gymnotidae give off electric discharges.

Compared with the Mormyridae, the family Gymnotidae comprises fewer species. Nevertheless, taken as a group they show a wider range of discharge patterns and frequencies, and between 2 and 1000 impulses/sec. have been reported (Grundfest, 1957).

In the course of the present study four species have been examined: *Gymnotus*

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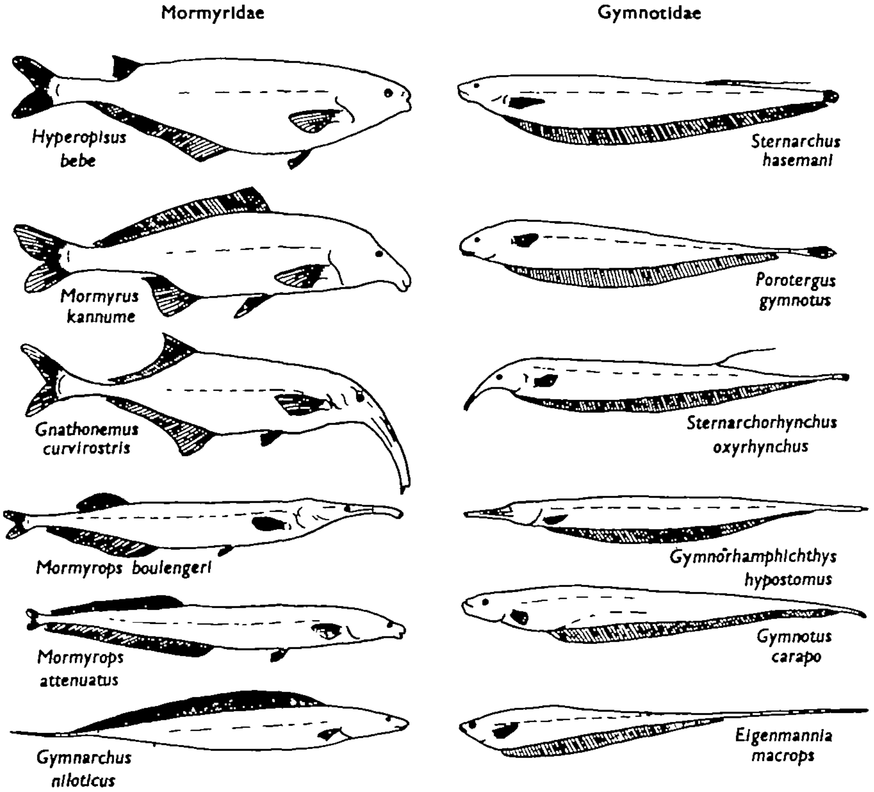
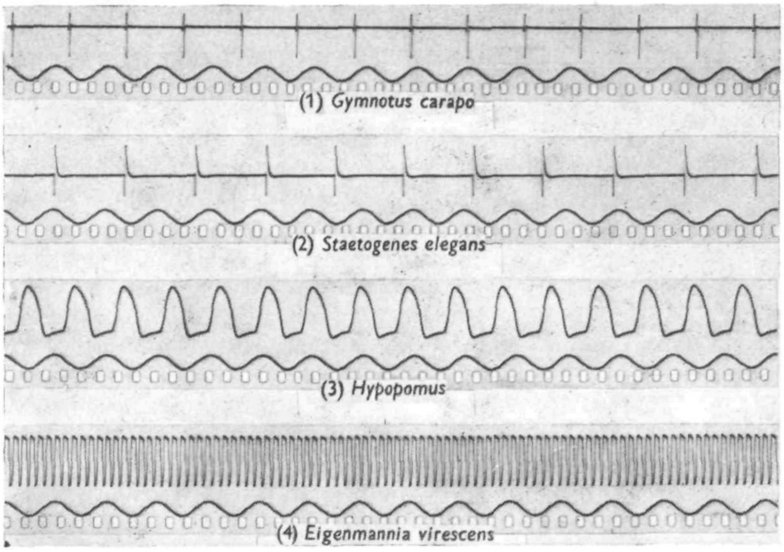
* In this respect there appears to be substantial agreement with a recent note on the subjcet by Moehres (1957).

*carapo*, *Eigenmannia virescens*, *Hypopomus brevirostris*, and *Staetogenes elegans*. Examples of the discharges of these fish are given in Text-fig. 6. It will be seen that they are of two types: those of *Eigenmannia* and *Hypopomus* which, apart from frequency differences, resemble the discharges of *Gymnarchus*, and those of *Gymnotus carapo* and *Staetogenes elegans*. The latter are brief and diphasic or polyphasic and, therefore, more like mormyrid discharges, although the basic discharge frequency is considerably higher and does not show so much variation with the state of excitation. However, I find the variation to be considerably greater than the 10 to 20 % reported by Coates, Altamarino & Grundfest (1954) as can be seen from Text-fig. 7; but the increase in frequency is not as persistent as in many Mormyridae.



Text-fig. 5. Representative types of the Mormyridae and the Gymnotidae. The convergent evolution between these unrelated families finds its expression in the electric discharges, the reduction of the tail fin, propulsion through an elongated unpaired fin, development of long snouts and several other features.

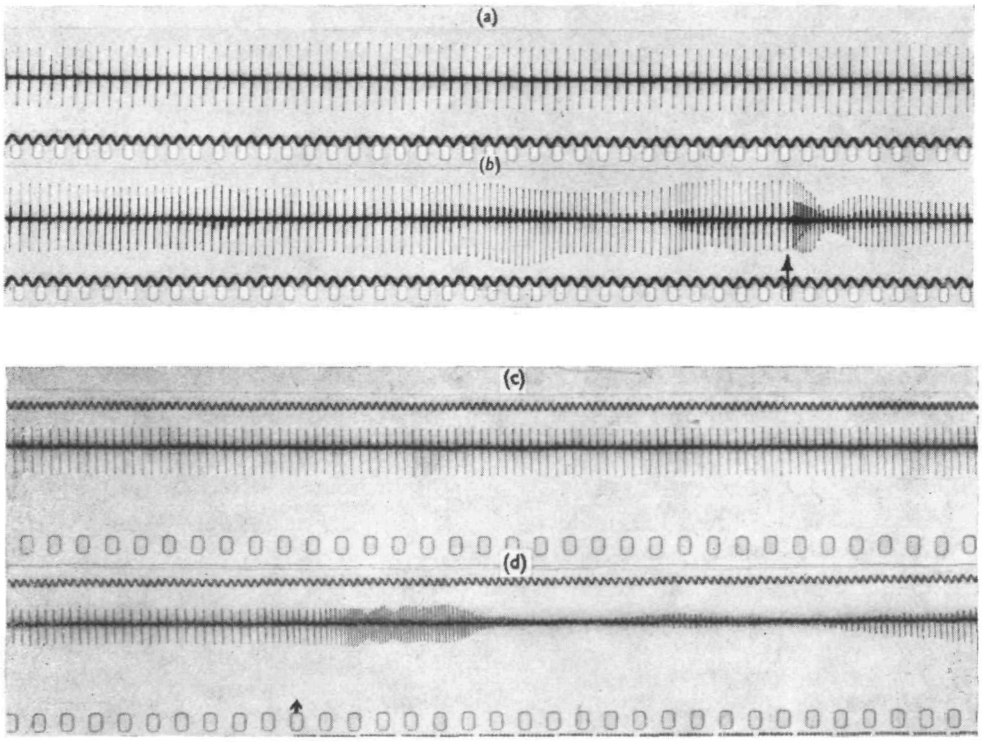
Different individuals of the species examined here show a considerable amount of variation in the frequency of their discharges. Twenty specimens of *Eigenmannia* (10–19 cm. in length) have been recorded; it has not been possible to relate this difference in discharge frequency to differences in size or to any other condition. A specimen of *Hypopomus* 27 cm. long recorded at 25° C. showed a frequency of about 60 pulses/sec., while a specimen of 23 cm. and at the same temperature discharged at the rate of about 90/sec. These differences have persisted over a period of weeks without much change. As in *Gymnarchus*, temperature is of direct influence on the discharge rate (Text-fig. 8).



Text-fig. 6. Discharges of four species of Gymnotidae at 25° C. (1) *Gymnotus carapo*, 15 cm. long. (2) *Staetogenes elegans*, 9 cm. long. (3) *Hypopomus brevirostis*, 27 cm. long. (4) *Eigenmannia virescens*, 15 cm. long. Note the short duration and diphasic nature of the pulses in the two upper records. Time marker 50 cyc./sec

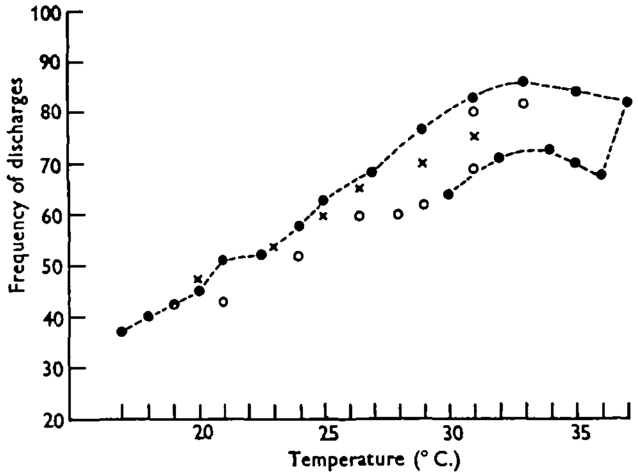
*Staetogenes elegans* has been of particular interest, because Ellis (1913) and Lowrey (1914) have reported that the submental filaments of this species are structurally identical with the tissue of an electric organ. However, this shy, nocturnal fish is not easily subjected to experimentation. In a normally illuminated room it seems to spend most of the time lying on its side on the bottom of its aquarium emitting regular diphasic pulses (Text-fig. 6), similar to those of *Gymnotus carapo*. No subsidiary activity has, so far, been noted from the head region under such conditions. In a dark room the fish swims actively in mid-water and feeds; as soon as the lights are switched on it rolls over on its side and sinks to the bottom, possibly simulating a dead leaf.

A number of attempts have been made to plot the electric field which is set up with each discharge by *G. carapo*. The fish was placed in a fold of a nylon stocking which was kept taut by two thin Perspex rods clamped the distance of the length of a fish apart and dipped in near the surface of the water in a large shallow tank. Although this prevented the movement of the fish to some extent, after a while most specimens began to struggle and a complete plot for any one specimen was not achieved. By placing one electrode successively along various levels of the fish, and fitting a second electrode to a pantograph and drawing for each position the lines of equipotential a picture of the field could be obtained. As the example in Text-fig. 9 shows, the line of equipotential which is normal to the long axis of the body lies further foward in *Gymnotus* as compared with *Gymnarchus*.

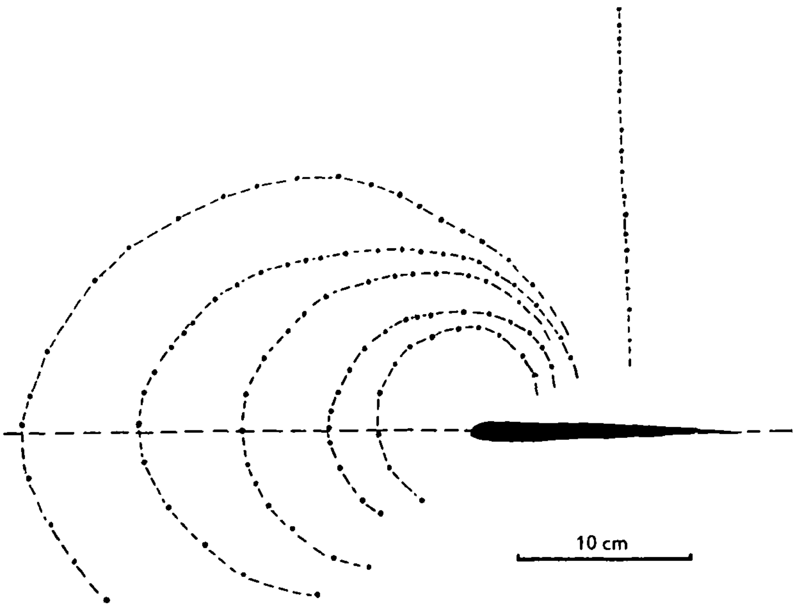


Text-fig. 7. Discharge frequency of *Gymnotus carapo* before and after excitation. (*a*) A fish 17 cm. long at 25° C. discharging at the rate of 60 pulses/sec. (*b*) After excitation the discharge rate goes up to 100 pulses/sec., and for brief periods after being touched with a glass rod ( ↑ ) up to 200 pulses/sec. (Continuous record.) (*c*) Another fish, 13 cm. long at 20·5° C. discharging at the rate of 43 pulses/sec. when at rest. (*d*) The same fish after a piece of earthworm has been dropped in front of it ( ↑ ). During the next ¼ sec. the discharge rate goes up to 100 pulses/sec. Time marker 50 cyc./sec.

*G. carapo* is a hardy fish which depends partly on atmospheric respiration and is a voracious feeder. Preliminary experiments were, therefore, undertaken to test its suitability for conditioned reflex experiments. This fish shows similar sensitivity towards stimuli induced by a magnet, an electrostatic charge or the introduction of a conductor into the water of its aquarium as have been described for *Gymnarchus*, but unlike *Gymnarchus* it seems to rely to a greater extent on its eyes. Training of this fish was therefore undertaken in a semi-dark room, and the critical tests, during which the reactions of the fish were automatically recorded, were carried out in complete darkness. The arrangement is illustrated in Text-fig. 10*a*. An all-glass



Text-fig. 8. The effect of temperature on the discharge frequency of *Gymnotus carapo* (three specimens). (1) A fish of 22 cm. long (○) increasing its frequency as the temperature is increased. (2) A fish of 15 cm. (×) decreasing the frequency with decrease of temperature. (3) A fish of 13 cm. (●) responding with increased frequency to an increase of temperature from 17 to 33° C. Further warming to 37° C. led to a slight drop. Subsequent cooling produced lower values as compared with previous readings at the same temperature. The temperature was changed in all instances at the rate of 1° C. per 15 min.



Text-fig. 9. Plot of the electric field round the head of a *Gymnotus carapo*. The lines of equipotential are indicated.

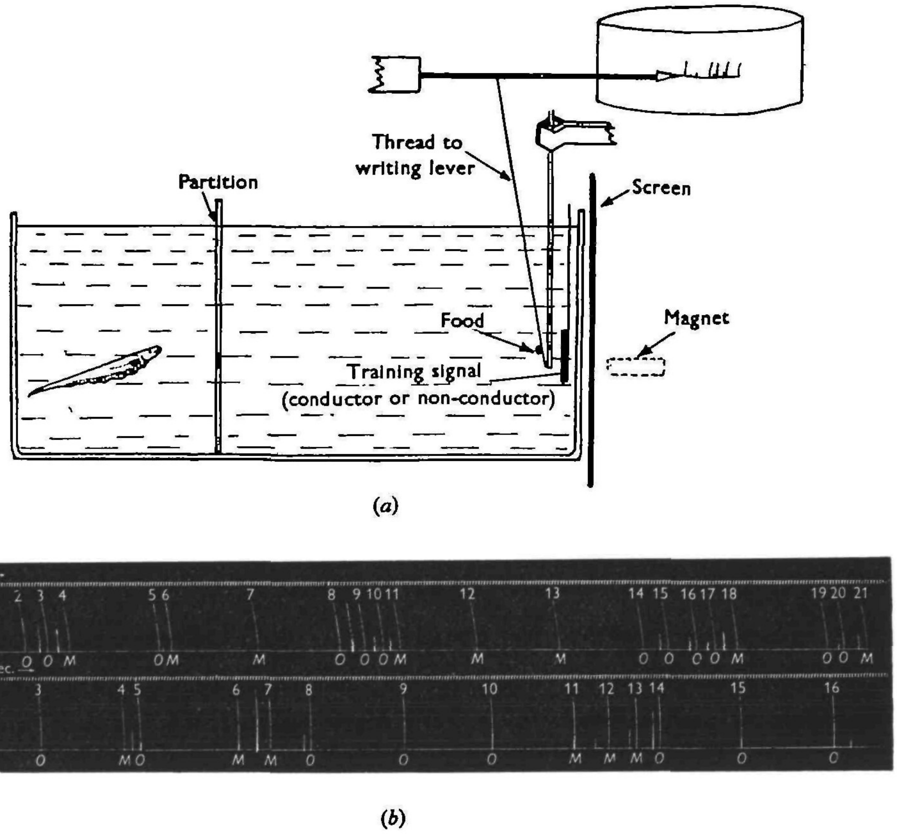
aquarium was divided by a partition into two halves. Before the trial the fish was placed in one half while a small piece of earthworm on a thread was introduced into the other half. The thread was stretched between a Perspex rod which dipped into the water and a recording lever writing on a smoked drum. When the partition was removed, which was synchronized with the start of the recording drum, an unconditioned fish would after a while find and accept the food, and the pull on the thread was registered on the drum. The training was of the reward-punishment type. It was found, however, that the method frequently used as punishment in similar fish-training experiments, namely, a knock with a glass rod on the snout, had no effect in the case of *Gymnotus carapo*. Even after quite hard knocks the fish attacked the glass rod and persisted with these attacks continuously for up to 10 min. When after several days the fish had not learned to respect the rod, this was replaced by a T-shaped 'punishment' device. The vertical arm of the T was a handle of Perspex, and the cross-bar a thin piece of aluminium 10 cm. long. At first it was sufficient to dip the metal just below the surface of the water above the fish to chase it away. In prolonged trials the original effectiveness of this method faded to a certain extent, but even in hardened animals a slight touch was adequate as the maximal punishment.

A well-trained fish usually took the food within 4 to 5 sec. on presentation of a positive stimulus, and if it did not approach the food within 30 sec. (initially 60 sec.) during a negative stimulus, this was counted as the correct response. When small pieces of food were used as reward up to sixty trials could be carried out each day; some fish had learned their task within 2 days and showed little or no improvement after that time.

The discrimination of conductors from non-conductors was tested first. Several fish, in separate experiments, were made to take the food when it was presented in front of a Perspex disk 5 cm. in diameter, and not to take it in the presence of a 5 cm. aluminium disk. Having learned this task under ordinary light conditions the fish were presented with the choice between the aluminium disk and a Perspex disk painted with aluminium paint (insulator). There was no hesitation and the insulator and conductor were distinguished as before. Since a number of different disks of both types were used, and since both types were practically indistinguishable to our eye, this seemed to indicate that the conditioning stimulus was not optical in nature.

The experiments were then continued in complete darkness. The Perspex disk could be substituted by a glass disk or a Tufnol disk, and the aluminium disk by any metalic disk without affecting the reactions. One may, therefore, conclude that chemical stimuli played no role in this training and that the operative stimulus was electrical in nature.

The converse experiment, using the conductor as the positive stimulus and the non-conductor as the negative stimulus, was carried out on two other specimens of *G. carapo*. Initially the behaviour of the fish towards this 'positive' stimulus was different: it approached the metallic disk slowly and in a fighting posture (strong lateral curvature and periodic thrashing of the body). The disk was frequently attacked and bitten before the worm was accepted. But the use of hungry fish and the placing of the disk in the early trials at some distance from the food soon resulted in good performance and learning. Paradoxically, at some intermediate stage the attacks were transferred to the Perspex disk.



Text-fig. 10. (*a*) Arrangement for training experiments to conductors and non-conductors and to a stationary magnet (*b*) Record of two specimens of *Gymnotus carapo* (I and II) conditioned to a stationary magnet. The numbers (1–20) upper record and (1–16) lower record indicate the beginning of each trial when a partition was removed in the aquarium giving the fish access to the food; simultaneously the recording drum was started. The food was presented on a thread, which was attached to a lever recording on a smoked drum the pull exerted by the fish when the food was accepted. *M* denoted the presence, *O* the absence of a magnet behind a screen near the food; the sequence was determined by the toss of a coin and is identical in both records. Fish I (upper record) had been conditioned to take the food in the absence of the magnet, and not to accept it within 30 sec. in the presence of the magnet. The first mistake occurred in the twenty-second trial (not on this record). Fish II had been trained in the opposite sense and was subjected to the same sequence of trials. The first mistake occurred in the sixteenth trial.

These results clearly indicate the suitability of *G. carapo* for training experiments; they further suggest (with the reservations made on p. 165) that the fish appreciates an electrical phenomenon and discriminates on this basis.

It seemed desirable to substantiate this view through experiments in which direct contact of metals and the water could be avoided. Since these fish, like *Gymnarchus*, respond to the movement of a magnet outside their tank, an attempt was made to train two fish to a stationary magnet, placed behind a screen close to the food source. A strong horseshoe magnet was used for this purpose. The set-up and procedure was essentially as in the previous training experiments. One of the fish was trained to accept food in the presence of the magnet, and to refuse it for 30 sec. when the magnet had been removed. With the second fish the training procedure was reversed. Again, to avoid any possible subconscious optical signals by the experimenter, the final tests were carried out in complete darkness. The results of such a test are given in Text-fig. 10*b*. Although mistakes occurred, the fish were clearly aware of the presence or absence of the magnet behind the screen. Usually both fish developed a 'stereotyped' path of approach towards the food; mistakes appeared to occur more frequently when, for some reason, there was a deviation from this path.

In these experiments, it must be assumed, that the flow of water caused by the fish's movement, or the movement of the fish's body in the magnetic field, produces potential differences which are appreciated by *G. carapo* (see also Lissmann & Machin, 1958).

## VI. DISCUSSION

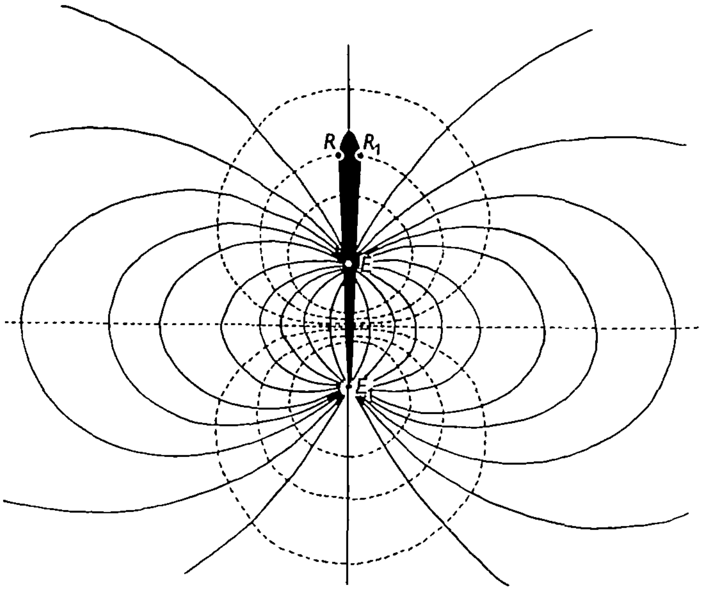
The theory of the function of electric organs suggested here implies that in a homogeneous aquatic environment the fish sets up an electric field which resembles that of an electrical dipole. Any object having a conductivity which differs from that of water may be expected to deflect the lines of force and will, if introduced into the water, disturb the original configuration of the field. It is assumed that the fish is able to sense this distortion of the field.

To test this theory a model was constructed consisting of two pairs of electrodes dipping into the water of a shallow tank. The first pair was connected to a beat-frequency oscillator and produced an electric dipole field comparable to that of a fish (Text-fig. 11). The second pair, corresponding to some hypothetical sense organs, was connected to an amplifier and an oscilloscope, and was placed at right angles to, and each member equidistant from, a line connecting the discharging electrodes. When both pairs of electrodes were carefully adjusted the recording electrodes were on a line of equipotential and no pulses were displayed on the oscilloscope. As soon as a piece of glass, metal or the human hand was now placed into the water in the vicinity of either electrode the pulses appeared on the oscilloscope. Also when a fish (non-electric) was introduced into the water its presence became visible on the oscilloscope whenever it approached the electrodes.

Although in a crude way this model may illustrate the mechanism used by electric fish, it also illustrates some of the difficulties: (i) both pairs of electrodes must be very carefully and rigidly adjusted to show the effect with any clarity; (ii) although the voltage of the discharges was higher than that recorded from weak electric fish, and although maximal gain was used on the recording side, the objects appeared detectable only at a relatively short range.

Nevertheless, it is useful to keep this model in mind when considering the possible anatomical and physiological counterparts in the fish body and the history of their origin.

While there may not be a single simple answer to the problem of the evolution of all electric organs, a number of unrelated forms have striking similarities in common. A comparative survey may, therefore, yield valuable information.



Text-fig. 11. Diagram of the electric field about equal charges of opposite sign. The lines of force (solid lines) and the lines of equipotential (dotted lines) are indicated. $E$ and $E_1$ correspond to the discharging electrodes in the model or the electric organ of a fish; $R$ and $R_1$ represent the recording electrodes or the hypothetical receptors.

### (*a*) *The discharge mechanism*

All available evidence suggests that independent evolution of electric organs in fish has taken place at least seven times. In the majority of cases embryology and innervation indicate clearly that the origin is from muscular tissue. As far as is known there is nothing in fish muscles which may point to the reason why in this class of animals alone muscle should be particularly predisposed to such a specialization. Although the regularity of myotomic arrangement should make a reconstruction into serial electroplates perhaps more feasible, it must be remembered that not only tail and trunk muscles have been incorporated into electric organs—as in the case of Rajidae, Mormyridae, *Gymnarchus*, the Gymnotidae, and probably also in *Malapterurus* (Johnels, 1956)—but also hypobranchial muscles (Torpedinae) and even eye muscles (Astroscopus) (Dahlgren, 1927). The origin and significance of the electric organs in the submental filaments of *Staetogenes elegans* (Ellis, 1913; Lowrey, 1914) remains obscure. In an inquiry about the causes of the evolution of electric organs it appears more profitable to consider the whole functional complex

—as depicted in the model experiment—rather than attempt to find the reason in the fish muscle alone.

It has been mentioned that in the model experiment rigid fixation of the electrodes appears essential if the proposed mechanism is to work. In an active, living animal such degree of rigidity would seem to be difficult to achieve. Yet there are indications that in electric fish some provisions have been incorporated which achieve this to a certain extent. This seems obvious in forms like *Gymnarchus* and the Gymnotidae which during most phases of active movement can keep the electric organ in line with the long axis of the body. Forward and backward propulsion and turning movements can be accomplished in both types through the undulation of a very long unpaired fin. The fact that it is the dorsal fin in the case of *Gymnarchus*, and the anal fin in the case of all the Gymnotidae may be accepted as one of the many striking features of convergent evolution between these two groups (Text-fig. 5). The view, frequently expressed, that *Electrophorus* is reduced to swimming through undulations of the anal fin, because its 'trunk muscles' have been used up and transformed into electric organs, appears somewhat one sided since other gymnotids, despite their very small electric organs, have the same method of propulsion. At the same time this type of swimming mechanism does not *per se* imply an electrogenic fish; e.g. no discharges could be picked up from *Xenomystus nigri*.

In *Gymnarchus* and some Gymnotidae a complete loss of the tail fin has occurred. In other Gymnotidae a considerable reduction of the tail fin has taken place, and parallel instances can be found amongst the Mormyridae, such as *Isichthys henryi* and *Mormyrops attenuatus* (Text-fig. 5), which swim essentially through synchronous undulations of dorsal and anal fin, both much elongated. No counterparts are known amongst the Gymnotidae which would correspond in general body form and swimming movements to the large majority of the Mormyridae. These seem to propel themselves in an essentially piscine manner through lateral oscillations of the tail fin. The muscles, however, which move this tail fin lie further forward than in other fish and anterior to the electric organ; their tendons run over this organ. The region of the electric organ itself would appear to be stiffened to some extent against lateral bending through the four longitudinal 'Gemminger's bones' (sometimes fused). Two possible reasons for the function of these unique structures may be put forward: (i) since consecutive myotomes of the caudal peduncle have been weakened by incorporation of muscular tissue into the electric organ, this region may require the special skeletal support of these bones; (ii) if the symmetry of the electric field around the longitudinal axis of the fish is to be preserved during swimming movements, these bones may contribute towards the rigidity of this region of the body. It would not appear implausible to ascribe to 'Gemminger's bones' both these roles.

Apart from the fish examined here it may be significant that another family of electric fishes, the Rajidae, have an analogous propulsive mechanism. It will be recalled that in swimming these fish trail the rather rigid tail with its electric organ symmetrically throughout the locomotory cycles executed by the pectoral fins.

*Torpedo*, on the other hand, does swim by means of sculling motions of its tail and makes no use of its pectoral fins for locomotion (Wilson, 1953). A similar mode of propulsion is used by *Astroscopus* (Dahlgren, 1927). Both these fish have cranial electric organs and the symmetry of the electric field will coincide with the symmetry of the fish's body except in the tail region. However, both are sluggish, bottom-living forms; if their—or their ancestor's—electric organ could be used for locating prey and other objects, the factor of maintaining a symmetrical field may not be so significant as in an actively hunting fish.

Whether similar speculations are applicable in the case of *Malapterurus* appears uncertain. The fish is not an active swimmer and when it swims it gives the appearance of a rather rigid sausage propelled by somewhat ostraciform tail movements. Three specimens of this species have been examined. None of them ever gave off the continuous electric pulses noted in the other species. When prodded they all produced a short train of strong, monophasic pulses (four to twenty). Otherwise they only discharged occasionally during feeding time, e.g. when a large worm was thrown into the water the fish would take it into its mouth, spit it out again, discharge, and then swallow the food. Nevertheless, it appears that a closer examination of the Siluridae would be profitable, because no intermediate forms between the strong electric *Malapterurus* and the other non-electric Siluridae have been found, a position which a few years ago had its close parallel in the Gymnotidae.

While one may thus assume that some mechanisms are incorporated in the general plan of these fish in order to maintain the symmetry of the electric field, these cannot be compared with the rigidity of the electrode system in the model. In fact, it can often be seen that the tip of the tail of a fish like *Gymnarchus*, when swimming backwards, may perform what looks like exploratory movements (see also Budgett (1901), p. 132, '*Gymnarchus* swims rapidly backwards...it may be seen to guide itself through the grasses by using this peculiar tail which it possesses as a feeler'). This type of movement is particularly noticeable in the early stages of training experiments when the fish often turns round and approaches the training site tail first, performing continuous 'scanning' motions with the tip of the tail. At this stage it is impossible to decide how far any proprioceptive information may be centrally integrated with electric information.

The intimate physiology and biochemistry of the discharges lies outside the scope of this paper. A considerable body of information has been accumulated in recent years (see Keynes & Martins-Ferreira, 1953; Grundfest, 1957), but insufficient comparative data are available on the mechanism of individual electroplates or their nervous control. The high frequency of discharges makes it appear unlikely that in all cases the discharge of an electroplate should be dependent on the arrival of a motor impulse.

In both the Gymnotidae and the Mormyriformes, two essentially different types of discharges have been found: (i) very regular, monophasic discharges of relatively long pulse duration and frequency independent of the state of excitation of the fish (*Adontosternarchus*, *Hypopomus*, *Eigenmannia*, *Gymnarchus*). The recorded frequencies vary between 60 and 940 impulses/sec. (ii) Complex di- or polyphasic pulses of more variable discharge rate and of very brief pulse duration (0·2 msec.

from the whole organ in *Petrocephalus*). Each pulse is separated from the next by a relatively long interval. The frequency of the discharges can increase considerably with excitation of the fish, and it can also be completely suppressed by suitable stimuli. The frequency range is between 0 and 200 impulses/sec.

At this stage no satisfactory explanation can be offered for the possible reasons behind these two discharge types, and no correlation with life habits has been established.

### (*b*) *Receptor and integrating systems*

While the parallel between the discharges in the model and in the fish can be accepted, special difficulties are encountered in suggesting a suitable electrical receptor system which may serve as an analogue to the receiving electrodes in the model. On the other hand it must be pointed out that histologists for a long time have been at a loss in their efforts to find a suitable function for a number of sensory endings which are particularly common in electric fish or in closely related forms.

From a structural point of view the Mormyridae have been most carefully examined by a number of authors. Franz (1912, 1921), whose main conclusions have been rejected by later workers, has put forward an idea which is worth considering: 'A question for future research would be to consider whether perhaps the mormyrids themselves appreciate the electric shocks of members of their species, and thereby adjust their own behaviour; further whether the most peculiar structure of the epidermis affords protection for the internal organs against electric shocks' (Franz, 1921, pp. 140–1).

It is generally considered that in an electric field in fresh water the fish body acts like a relatively good conductor, enclosed in a less well-conducting membrane, surrounded by a bad conductor (Holzer, 1931, 1933; Spiecker, 1957). Although no experimental data appear to be available for Mormyridae, Franz's assumption that a thickening and layering of the epidermis would reduce the conductivity over the fish body does not seem unreasonable. As Marcusen (1864) has pointed out, this thick skin is rich in fat and contains many pores. Later examinations have shown (Stendell, 1914*a*, 1916; Franz, 1921; Berkelbach van der Sprenkel, 1915; Suzuki, 1932; Cordier, 1938; Gérard, 1940) that these pores lead through canals filled with a jelly-like substance to a variety of sense organs termed 'glandular sense organs' or 'mormyromasts'. These 'mormyromasts' are innervated by lateral line nerves and are particularly crowded at the snout and head region. They can be found over the whole body, except on the caudal peduncle, i.e. the region of the electric organ.* There appears little doubt that the enormous development of the 'mormyro-cerebellum' (enlarged valvulae cerebelli) can be correlated with the profusion of these sensory terminations. Conventional lateral line sense organs are also present in the Mormyridae but their numbers are unexceptional. Similar sensory endings have been described for *Gymnarchus* (Stendell, 1914*a*; Pehrson, 1945), and although the cerebellum does not reach the same dimensions as in the Mormyridae it is disproportionately large if compared with other fish.

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* Wright (1958) claims to have located an electrical receptor at the base of the dorsal fin in a mormyrid. However, alternative interpretations of his experimental findings seem possible.

The Gymnotidae are less well documented in this respect. However, Coates, Cox & Smith (1938), while examining a papilloma of the skin in *Electrophorus*, state that the normal epidermis is rather thick, twenty to thirty cells in depth, resting upon a well-developed basement membrane. Extending outwards at right angles to the surface of the body are found at short, regular intervals numerous prolongations of fibrous tissue passing as supporting septa outwards into the epithelium. Coates (1950) mentions some enlarged pores of the lateral line around the head of this fish. Although he states that he has been 'unable to find anything of particular interest beneath these pores' he suggests a connexion of some cranial receptors and the locating mechanism, since insulation of the head upset the orientation of a fish. His view that electro-magnetic waves, analogous to radar, are at work and that the fish is able to appreciate the time delay of outgoing and reflected waves (Coates, 1947) over a distance of a few inches appears unacceptable on physical and physiological grounds. Again, the cerebellum in gymnotids is a massive organ, but the neuro-histology is not sufficiently known in detail. The picture as a whole presented by the Gymnotidae, despite the scanty information of finer detail, does not appear unlike that of the Mormyridae. A comparative study of gymnotid brains and receptors would be clearly of great interest. The parallel evolution of electric organs and long snouts in both families (Text-fig. 5) tempts one to predict the occurrence of 'Schnauzenorgane' (Stendell, 1916) in both.

The first discussion of the possibility of an 'electric sense' appears to be that which arose from a misunderstanding of Wagner's (1847) paper by Boll (1873, 1875) and concerns Savi's vesicles in *Torpedo*. These completely encapsulated, round sense organs, 2 to 3 mm. in diameter, are found in great numbers, regularly spaced, beginning at the outer perimeter of the electric organ and extending to the snout and pectoral fins. They form part of the lateralis system of these fish. Boll rejects them as possible 'electric sense organs' because (i) electrical stimulation of the proximal nerve supplying these organs 'excites the activity of the electric organ neither more nor less than stimulation of any other sensory nerve'; (ii) analogous organs in the two other species of electric fish are not known.

Neither of these two arguments appears acceptable to-day. It is interesting to note that not only are the eyes poorly developed in most species of *Torpedo*, as they are in *Electrophorus* and *Gymnarchus*, but that a number of blind species are known with relatively smaller electric organs (e.g. *Typhlonarke*, Garrick, 1951).

The small, essentially serial caudal electric organ of the Rajidae has hardly been investigated from a biological point of view, although it can be made to discharge in a physiological experiment. The idea that the fish's prey may be stunned by such electric shocks is hardly tenable since many species are mollusc feeders. On the other hand the differentiation of the lateralis system, notably the ampullae of Lorenzini (also found in *Torpedo*) have attracted much attention. These grape-like vesicles are located some distance beneath the surface of the body and are in communication with the outside through long tubes, filled with a jelly-like substance. The 'mormyromasts' have often been likened to the ampullae of Lorenzini. After much inconclusive speculation and experimentation the balance of opinion to-day has shifted from the 'pressure receptor theory' towards the 'temperature receptor theory' (Sand, 1938; Hensel, 1955). Observations of the impulses along the afferent nerves of these organs have shown that they behave similarly to mammalian cold-receptors, and they have been shown to respond to temperature changes of 0·05° C. Before, however, accepting this interpretation as satisfactory three points should be cleared up: (i) why should a sensitive temperature receptor be located deep in the body, when it takes several seconds to transmit the temperature to that depth? (ii) The cranial innervation and the divergence of the canals from these organs suggest a receptor designed for a rapid point-to-point correlation of outside stimuli. It is difficult to see why temperature receptors should occupy such an exceptional position in the skate. (iii) What is the biological stimulus to which these organs are adapted to respond?

It is interesting that Franz (1912, p. 487), in discussing the cerebellum of fishes, notes that the mormyrid cerebellum—and also for unknown reasons the cerebellum of the sluggish skates—is disproportionately large. Even if the mode of subdivision of the cerebellum is different in teleosts and elasmobranchs, and the valvula cerebelli not typically represented in the latter, the pars auricularis ('restiform bodies') forms a corresponding centre (Kappers, 1906; Herrick, 1924); this part is said to be particularly well developed in the skates.

The main difficulty in accepting the ampullae of Lorenzini as electric sense organs derives from the fact that some fish are endowed with these sense organs without, apparently, possessing specific electric organs. This applies not only to elasmobranchs but equally to the Siluridae. Only one member of this family, *Malapterurus*, is known to possess an electric organ. Yet Siluridae are the only bony fishes known to possess typical ampullae of Lorenzini (Friedrich-Freska, 1930). The species *Plotosus anguillaris*, in which these organs have been discovered, is, perhaps significantly, one of the few marine Siluridae. In freshwater catfishes Herrick (1901, 1903) has discovered the 'small pit organs'. He states that 'the aperture by which the pit communicates with the surface is a very minute pore'...and 'the pore may run downward as a straight tube of considerable length before dilating into the sac-like cavity of the pit'. Again, these organs are innervated by lateralis nerves and glandular or mucous cells are found in close proximity to the sense organs. The resemblance to 'mormyromasts' is unmistakable.

Moreover, although these catfishes do not possess an electric organ their great sensitivity towards electrical stimulation has been noted by several observers (Parker & van Heusen, 1917; Hatai, Kokubo & Abe, 1932; Abe, 1935; Kokubo, 1934; Uzuka, 1934); Parker & van Heusen (1917) also note that these fish respond to an electro-magnet.

Another significant feature seems to be the fact that next to the Mormyridae, the Siluridae show the most specialized development of the valvula cerebelli (Kappers, 1906; Berkelbach van der Sprenkel, 1915).

No comparable data seem to be available for *Astroscopus*; it is interesting, however, that larval pelagic specimens do not possess electric organs. The transformation of the eye muscles into electric organs can be related to the change to a benthonic life habit in the adult fish which has a number of striking adaptations suggesting an environment of poor visibility (Dahlgren, 1927).

### (c) *General considerations of the lateralis system*

Although the general picture of the evolution of electric organs is by no means clear to date, the crowding of coincident features does not appear without significance. It may seem that the possession of suitable receptors, rather than the ability to transform muscles into electric organs, is the major prerequisite for this step in evolution.

It is therefore of interest to consider the properties and mode of action of the lateral line sense organs in their more generalized form. The fact that they serve as mechano-receptors seems to be universally accepted (Dijkgraaf, 1933, 1952; Sand, 1937; Katsuki, Yoshino & Chen, 1950, 1951 *a*, *b*). The transformation of such a receptor, which in its most primitive form projects over the surface of the body and is covered by a jelly-like cupola, into an electro receptor which is sunk below the surface, may appear a formidable difficulty. Even if we accept the perception of small water currents, vibrations and pressures as the primary function of the superficial lateralis organs, and also the reasons advanced by Dijkgraaf (1952) for their subsequent inclusion into lateral line canals, it must be remembered that Regnart (1931) has shown that the lower limits of perception of electric currents by fish (codling) are dependent on the presence of such lateral line organs.*

Given the ability to respond to electric stimuli the next question which arises would be as to the nature and origin of electrical stimuli any pre-electric fish may encounter. In this respect our knowledge is very incomplete, but one source which could be suggested is the muscular action potential of prey, predator, members of the same species and of the fish itself†. In an aquatic environment the recording of such action potentials some distance away from the animal presents no special difficulties. Text-fig. 12 shows such electrical disturbances recorded from an eel (*Anguilla vulgaris*, 38 cm. long) in a shallow tank. In the middle of the tank were placed two bricks between which the fish was sheltering. Electrodes, 12 cm. apart and 1 cm. long, were fixed more or less parallel to the posterior end of the animal and 10 cm. from it. Whenever a hand was passed over the tank, casting a shadow, the eel performed a jerk, and what appeared to be a muscular action potential was displayed on an oscilloscope. This procedure could be repeated up to ten or twelve times in rapid succession, after which the animal ceased to respond. After a short while the same phenomenon could be evoked again. It can be imagined, particularly in a gregarious species, that the perception of such electrical disturbances could be of survival value. Recordings of spike potentials, coincident with the breathing movements of *Petromyzon marinus*, have also been picked up from the surrounding

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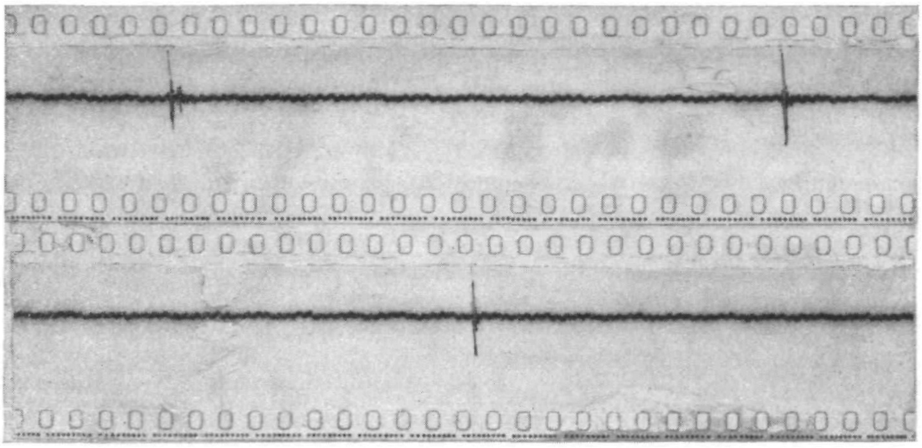
* I am aware that these findings have not been universally accepted, e.g. Spiecker (1957). Regnart used nerve section, Spiecker superficial application of anaesthetics to eliminate this sense; moreover, Regnart is concerned with the 'primary reaction' (lower threshold) and not with 'galvanotaxis'.

† Hoagland (1935) considers the possible role of the lateral line as proprioceptor.

water by Kleerekoper & Sibakin (1956). We have no reason for believing that our electronic recording devices may be superior to a fishes receptor. Whether fish, having evolved great sensitivity towards electrical stimuli, may respond to other types of electrical phenomena of a magnitude likely to arise in nature, will be considered in another paper (Lissmann & Machin, 1958).



Text-fig. 12. Muscular action potentials recorded from an eel (*Anguilla vulgaris*) at a range of about 10 cm.; these could be observed when the resting fish, in response to visual stimulation, performed a sudden movement. Time marker 0·1 and 0·01 sec.

In the absence of any precise experimental evidence one can only surmise that, like other acoustico-lateralis sense organs, such electro-receptors will show a resting discharge, and that the frequency of the impulses may be varied by ascending and descending electric currents (Löwenstein, 1953). In the course of evolutionary transformation a stage of double specificity—to mechanical and electrical stimuli—must be postulated. The details of the mechanism by which the sensory cells of the labyrinth and the lateral line are excited are still not perfectly understood, but the microphonic potentials show a close association of mechanical and electrical events. The view that such voltages are generated by piezo-electric properties of the cupola seem to have been abandoned (Jielof, Spoor & de Vries, 1952). On the other hand, it has been suggested that the endolymph may play a significant role (Jensen, Koefoed & Vilstrup, 1954), since it contains a fair amount of hyaluronic acid. This solution, when mechanically displaced in a tube, sets up electrical flow potentials. Hyaluronic acid is also present in the jelly which fills the lateral line canals of fish (Katsuki, Mizuhira & Yoshino, 1952), though apparently not in the cupolae of lateral line receptors. Whether the jelly-like substance which fills the tubes leading to 'mormyromasts' and similar sense organs contains solutions exhibiting the phenomenon of flow potentials is not known. In view of the electrical nature of the stimulus there appears no need to postulate any special properties of this substance except electrical conductivity.

### (*d*) *Conclusion*

In the absence of any existing, coherent theories about the evolution of electric organs, and about the function of weak electric organs, the speculative picture presented here may fill a gap.

It is imagined that the first essential feature in the process of evolution of electric organs was the possession of receptors sensitive to electric stimuli. At an early stage this sensitivity may be regarded as an incidental, later a subsidiary and finally the specific function of such sense organs. On structural and functional grounds the lateral line receptors seem to fit the requirements best. Parallel with their differentiation the evolution of electric organs from muscular tissue may be postulated. The muscular action potential can be assumed to have been an initial stimulus source. Environmental conditions which can be expected to favour this trend in evolution would be those that preclude the normal functioning of other receptors (e.g. turbidity of water).

The weak electric fish discussed here represent already very advanced, highly specialized forms. The theory of the use of their electric organ offered in this paper suggests that these fish are able to use the information arising from distortions—caused by various outside sources—of the electric field which they themselves so regularly produce. The fact that electric fish have shown themselves extremely sensitive to minute electric influences produced experimentally, and that such experiments could not be repeated with non-electric fish, indicates that the great sensitivity of electric fish is related to the emission of electric discharges. Both on the effector and receptor side the central nervous system shows great specializations. The nervous mechanisms of the effector component have been recently explored in various species (Fessard & Szabo, 1953; Szabo, 1954, 1955). The 'mormyrocerebellum' and similar structures can be considered essentially as the relevant sensory integrating systems.

However, this specialization, once it has begun, does not only involve the organs of this one reflex arc. New locomotory mechanisms, new epidermal adaptations to electrical conductivity, etc., may follow, so that finally it can be imagined that such a fish, living in a private, electric world of its own, receives a variety of information through sense organs distributed over the surface of its body which may be likened to an 'electro-receptive retina'. The effectiveness of stimuli impinging on this retina can be expected to be enhanced if the epidermis in which they are embedded has improved insulating properties.

The striking elongation of the body in some freshwater forms can, in part, be regarded as an expression of the tendency to extend the effective range of this mechanism, e.g. the viscera proper occupy a space a little longer than the length of the head in many Gymnotidae (Text-fig. 5); they can be as short as one-eighth of the total length with the position of the anus anterior to the level of the eyes (Schlesinger, 1910). As the number of serial electric elements is increased, and thereby the voltage of the discharge, so a stage will be reached when 'objects', which previously could only be located, can now be stunned and swallowed.

In many details the views expressed in this paper can be subjected to a critical test by anatomical, histological and experimental investigation. On the outcome must depend the acceptance or rejection, in whole or in part, of the theories which are here tentatively suggested.

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## SUMMARY

1. The electric discharges of *Gymnarchus niloticus* and of representative species of seven genera of the Mormyridae have been examined in their natural habitat in Africa and in the laboratory.

2. Comparable investigations of the South American Gymnotidae have shown the existence of two discharge types in both these unrelated fish families.

3. The first type of electric discharge consists of very regular sequences of continuously emitted, monophasic pulses, varying from species to species in frequency, and within narrower limits from individual to individual.

4. Fish emitting this first type of pulses include *Gymnarchus*, *Hypopomus* and *Eigenmannia*. The frequency range for these fish lies between 60 and 400 discharges/sec.

5. The frequency does not alter with the state of excitation of the fish. The duration of individual pulses is relatively long, i.e. 2–10 msec.

6. The second type of discharge is less regular in frequency, the pulse duration much shorter and the pulse shape more complex. The individual discharge from the whole electric organ lasts about 0·2 msec. in *Petrocephalus*.

7. This type of discharge is found in all the examined species of the Mormyridae and in such forms as *Gymnotus carapo* and *Staetogenes elegans*.

8. The basic discharge rate of a resting mormyrid is somewhat variable and not strictly rhythmical. It usually lies between 1 and 6 pulses/sec.

9. Stimuli which excite the mormyrids cause an increase in the discharge frequency. The recorded maximum is about 130 pulses/sec.

10. Suitable stimuli can inhibit the discharges of the Mormyridae for prolonged periods.

11. In *Gymnotus carapo* and *Staetogenes elegans* the basic discharge rate is higher and of regular rhythmicity. Depending on temperature the frequencies lie between 30 and 87 pulses/sec. When these fish are excited the frequencies are increased up to 200 pulses/sec. for a short time.

12. The shape of the electric field, which is set up with each pulse around the fish, has been examined.

13. A theory has been proposed which suggests that these fish, by means of their electric pulses, can locate objects if their electrical conductivity differs from that of water.

14. These fish have shown themselves extremely sensitive to influences affecting the electric field. This has been studied by applying artificial electric stimuli, by studying the effects of conductors and non-conductors introduced into the field, and the reactions towards magnetic fields and electrostatic charges.

15. Conditioned reflex experiments with *Gymnarchus niloticus* and *Gymnotus carapo* have shown that these fish can detect the presence of a stationary magnet, and that they can discriminate between conductors and non-conductors.

16. The prey of these fish does not appear to be affected by the discharges. *Inter alia*, the electric pulses have a social significance.

17. This locating mechanism may be considered as an adaptation to life in turbid water.

18. Gymnotidae and Mormyridae (taken to include *Gymnarchus*) show striking features of convergent evolution.

19. Unusual locomotory adaptations such as swimming by means of the dorsal fin (*Gymnarchus*), the anal fin (Gymnotidae) and 'Gemminger's bones' (Mormyridae) may be considered as a means which tends to make the axis of symmetry of the fish and of its electric field coincide during active movements.

20. A new theory for the evolution of electric organs has been suggested. A major prerequisite appears to be a receptor sensitive to electrical stimulation.

21. It is suggested that special sensory and nervous differentiations of the lateralis system ('mormyromasts', valvulae cerebelli) are concerned with the perception and integration of electric stimuli.

22. Muscular action potentials have been recorded in the water at some distance from non-electric fish.

23. The easiest explanation for the evolution of strong electric organs would appear to start from such muscular action potentials, and proceed via weak electric organs used for orientation, to the powerful offensive and defensive electric organs.

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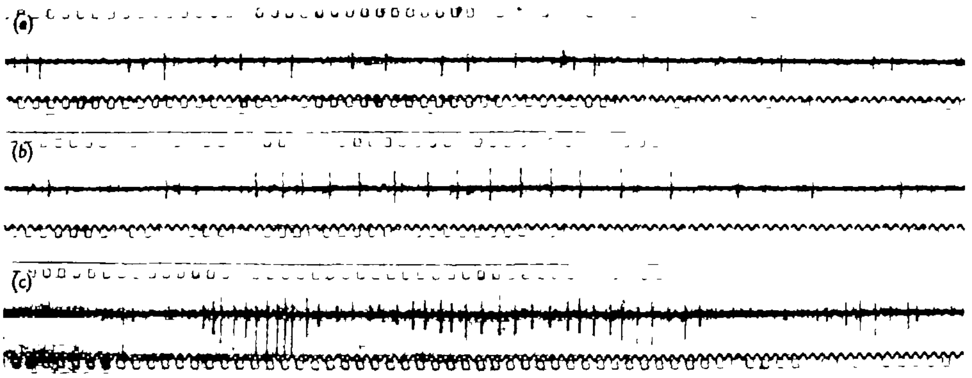

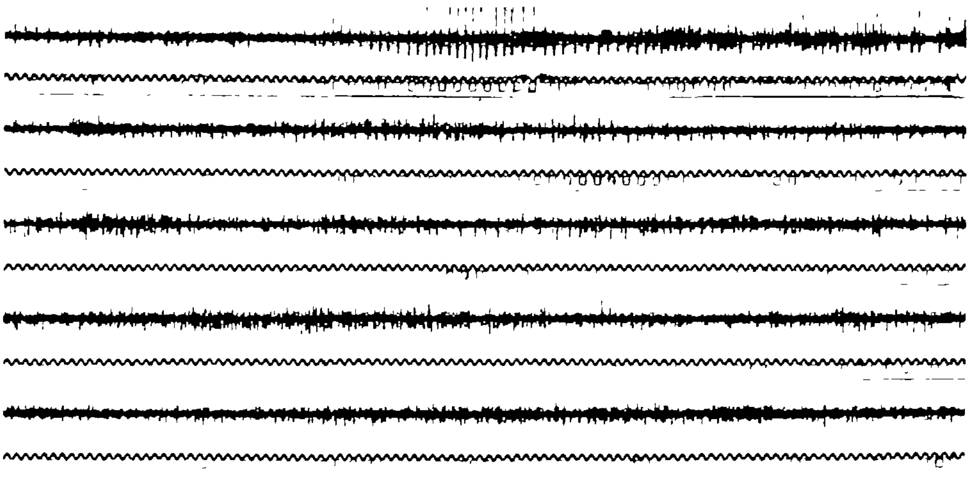

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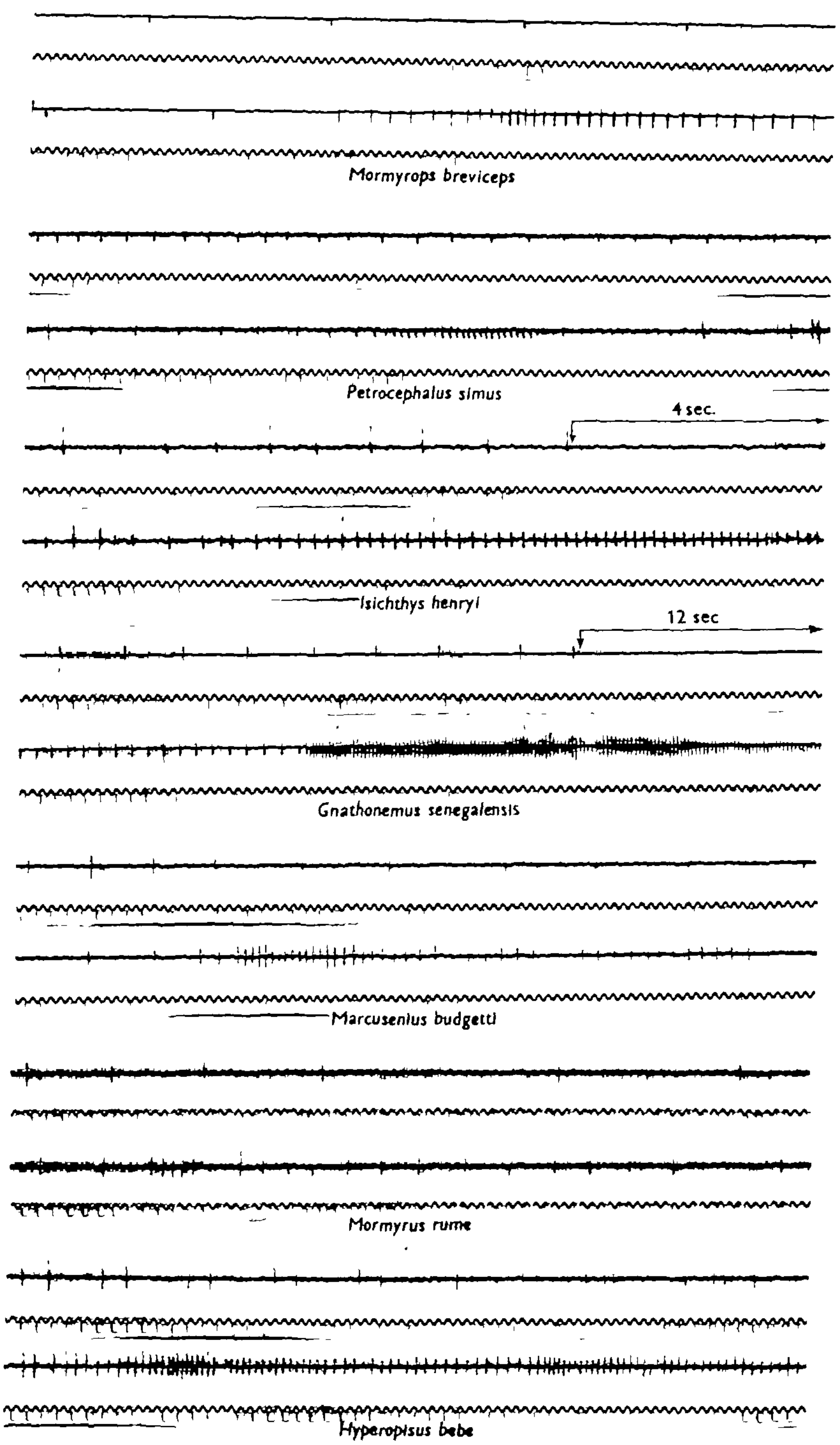

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## EXPLANATION OF PLATES 5 AND 6

### PLATE 5

1. Electric discharges recorded in African rivers (Black Volta (*a*, *b*), Kamba (*c*)). (*a*) The record indicates apparently three resting specimens discharging at a slow rhythm, of about 3 to 4 pulses/sec. (*b*) The impulses of a single, resting specimen which showed periodic acceleration of the discharges . (*c*) Pulses of frequencies of 20–50/sec. usually remain in evidence only for a short time and suggest an actively swimming specimen. Time marker 50 cyc./sec.

2. Recording of electric discharges from a small pool in the dry season. It contained species of *Petrocephalus*, *Marcusenius*, *Gnathonemus* and *Hyperopisus*. The discharges remained in evidence throughout the period of observation. Time marker 50 cyc./sec.

### PLATE 6

Discharges of representatives of seven genera of the Mormyridae, first at rest (upper record) then excited (lower record). Note the great increase in the frequency of the discharges with excitation. The upper and lower records are continuous in each case, except for *Gnathonemus senegalensis* and *Isichthys henryi*. In the former there was a period of 12 sec. during which the fish did not discharge while the experimenter approached the aquarium and was leaning over it before touching the fish with a glass rod. Similarly, *I. henryi* did not discharge for 4 sec. Note also the grouping of discharges into pairs prior to stimulation of *Hyperopisus bebe*; this has also been recorded in the rivers both during slow and fast discharge frequencies. Time marker 50 cyc./sec.