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The larval electric organ of the weakly electric fish *Pollimyrus (Marcusenius) isidori* (Mormyridae, Teleostei)

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Summary

The larval electric organ of *Pollimyrus isidori* consists of four longitudinal tubes, a dorsal and a ventral pair, which begin behind the skull, end at the beginning of the caudal peduncle and show myotomic segmentation. The elementary units are, apparently, transformed muscle fibres called electrocytes. They are shorter and thicker than muscle fibres, with long stalks and are found in the medial part of the deep lateral muscle. Electron microscopy reveals a clear difference between the anterior and posterior face of the electrocyte. Anteriorly, deep linear invaginations of the surface membrane together with many small vesicles of about 100 nm diameter can be seen. Posteriorly, many plasma membrane invaginations and vacuoles are found together with numerous cytoplasmic organelles – pleiomorphic nuclei, Golgi apparatus, oblong mitochondria and multivesicular bodies. The stalk originates at the posterior face and the nerve terminals are situated at the distal end of the stalk. In the electrocyte, myofibrils, similar to those found in muscle fibres, can be detected with clearly visible Z lines but with only a suggestion of H zones. Two bundles of myofibrils can be seen arranged orthogonally in the electrocyte. Strong acetylcholinesterase activity was found on the anterior face and on the innervated stalk. Under the given recording conditions the overall discharge amplitude of the larval electric organ reaches a maximum of about 100 mV peak to peak. The pulse duration is 1 millisecond and the main phase is head-positive.

Introduction

Myofibrils have been found in the electrocytes of adult mormyrids: this observation has led several authors (Ogneff, 1898; Schlichter, 1906; Dahlgren, 1910) to the conclusion that these cells develop from muscle tissue. Szabo (1957b) found parts of the deep lateral muscle, rostral to the adult organ of *Gnathonemus*, replaced by

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connective tissue and concluded that the electric organ had developed from this part of the lateral muscle. Ontogenetic information about the origin of the electric organ of mormyrids is incomplete because of the difficulty of obtaining larvae from the field. Preliminary results based on sparse material (Szabo, 1960, 1961a) indicate that the electrocytes develop from the transformation of muscle fibres.

The recent identification of the environmental factors leading to gonad maturation and spawning in these fish (Kirschbaum, 1975) made a developmental study of *Pollimyrus isidori* possible. Both the ontogeny of the electric organ and the development of the electric organ discharge (EOD) were followed in detail. The development of the EOD has shown that in young larvae a characteristic larval EOD first appears (Kirschbaum and Westby, 1975; Westby and Kirschbaum, 1977a) which is followed later by the adult discharge of opposite polarity. Spinal cord sections, electric field measurements, and micro-injections of curare (Westby and Kirschbaum, 1977b) together with an ontogenetic study of the adult electric organ (Kirschbaum, in preparation) have shown definitely that the *larval* discharge arises from a *larval* electric organ situated in the deep lateral muscle. This organ could be identified histologically as consisting of transformed muscle fibres (Kirschbaum, 1977). The larval electric organ and the adult electric organ – the well-known electric organ of mormyrids – are apparently homologous structures, of which the larval organ is the more primitive one. This is the first example of two distinct evolutionary steps in the development of electric organs existing simultaneously in the same species. In skates different evolutionary steps could also be found (Ewart, 1892; Engelmann, 1894) but they exist in different but related species. In this paper we describe the anatomy of the larval electric organ of *Pollimyrus isidori* and the cytology of the larval electrocytes. This should constitute a basis for the comparison of the ultrastructure of the larval electrocyte of *Pollimyrus* and that of the electrocytes of other electric fish already described (Luft, 1956, 1957, 1958; Mathewson *et al.*, 1958, 1961; Wachtel *et al.*, 1961; Bruns, 1971; Waxman *et al.*, 1972; Schwartz *et al.*, 1975; Machado *et al.*, 1976). These investigations together with ontogenetic studies concerning both the larval and the adult electric organ of *Pollimyrus* (Kirschbaum, in preparation) will, we hope, enable us to understand how the highly specialized electrocytes of mormyrids have evolved from the more primitive electrocytes of the larval electric organ.

Material and methods

The larvae of the mormyrid fish *Pollimyrus isidori*, formerly *Marcusenius isidori* (Taverne, 1971) we used in this study came from different spawnings which had taken place over a period of more than 2 years in our laboratory (Kirschbaum, in preparation). These larvae were raised and some of them reached maturity after about 1 year.

The histological investigations were done with Bouin-fixed and paraffin-embedded material. The whole fishes were serially sectioned, 7 μm thick, either transversely or sagittally, and then stained with Azan stain (Heidenhain). Paramedian cryostat sections (16 μm) of fresh larvae were used in order to study acetylcholinesterase (AChE) activity. AChE activity of the sections was

revealed with the modified thiocholine method of Koelle (Tsuji, 1974). Incubation time was 10 min at pH 5.0. The sections were counterstained with toluidine blue. The controls with butyrylthiocholine iodide were negative and those with iso-OMPA (10^{-5} M) were positive. For electron microscopy the whole larvae were fixed either in a primary fixative of a 2% glutaraldehyde solution (1 h in the cold) in Palade or Sjöstrand buffer at pH 7.2 and then secondarily fixed in a 2% osmium tetroxide Palade buffered solution (1 h in the cold) or the larvae were fixed in the 2% osmium tetroxide solution (Palade buffer at pH 7.2) as primary fixative. Following fixation, the tissue was dehydrated in graded concentrations of ethyl alcohol and embedded in Araldite.

The position of the electrocytes was studied first with light microscopy using 1 μm sections stained with toluidine blue in sodium borate. Thin sections were placed on uncoated copper grids, stained with an aqueous solution of uranyl acetate and lead citrate (Reynolds, 1963) and examined with a Siemens 102 electron microscope. Measurements of the overall EOD activity were made on intact fish in a small glass recording cell. The cylindrical cell was fitted with a pair of platinum recording electrodes sealed into its extremities. For the present study a 1 ml cell filled with water of constant conductivity (650 μS/cm) was used. All recordings were made at 27° C ± 0.05° (see Westby and Kirschbaum, 1977a for further details). The cell output was amplified with low noise equipment and conventional recording and display apparatus was used. The maximum background recorded noise level was 8 μV peak to peak.

Results

Gross anatomy of larval electric organ

The larval electric organ of *Pollimyrus isidori* is found only in larvae. It is seen for the first time in 8 mm long (8 day old) fish and degenerates early in the ontogeny of the fish. The adult organ begins to differentiate in 10 mm long fish and is functional for the first time in about 15 mm long larvae (Westby and Kirschbaum, 1977b; Kirschbaum, in preparation). Fish between 15 and 20 mm long possess both functional organs (see Fig. 21). The larval organ then begins to degenerate and in 25 mm long fish only the functional adult organ can be found.

The larval electric organ of 12 mm long (32 day old) larvae extends from the edge of the skull to the end of the dorsal fin (Fig. 1). It consists of four tubes, two dorsal and two ventral, which are situated in the medial part of the deep lateral muscle (Fig. 4). The dorsal and the ventral tubes are limited in the medial plane by the backbone and connective tissue. The horizontal myoseptum and muscle fibres separate the dorsal from the ventral pairs in the horizontal plane. The anterior part of the ventral tube is limited considerably by the body cavity (Fig. 1). The electrocytes, which constitute the electric organ, are arranged in parallel in the myotomes (Fig. 2). Muscle fibres as well as electrocytes are found in each myotome (Fig. 3). On the dorsal, ventral and lateral sides of the myotome there are what appear to be intermediate stages between muscle fibres and electrocytes, for example cells thicker and shorter than muscle fibres, but without stalks. It is therefore difficult to give the exact limits of the larval electric organ (Fig. 4). In the outer part of the myotome, where only muscle fibres are found, a typical myosept is present (Fig. 3), which is replaced at the level of the electrocytes by a large quantity of loose connective tissue, which separates the different rows of electrocytes. The

electrocytes in each myotome are in parallel, but they are oriented at about 45° to the longitudinal axis of the fish. They are 70–100 μm long and about 30 μm wide. They possess a long stalk (Figs. 3 and 5) at the posterior face. The stalk does not always make contact with the centre of the posterior face and there seems to be a tendency for the stalk to originate on one side of the electrocyte: on the ventral side in the ventral part of the myotome, and on the dorsal side in the dorsal part of the myotome. The stalk can be nearly as long as the electrocyte and it extends posteriorly into the space filled with loose connective tissue separating the rows of electrocytes.

Cytology of larval electrocytes

The most striking features of the cytology of the larval electrocytes of *Pollimyrus* studied here were the extensive membrane invaginations of both the innervated and non-innervated faces, the posteriorly originating stalk and the restriction of all organelles to the cell surface.

At the anterior face, deep linear invaginations of the cell surface are found (Fig. 7) which might represent the T-system of muscle fibres. The cytoplasm of this face contains few cytoplasmic organelles (nuclei, mitochondria) but many small vesicles of about 100 nm in diameter (Figs. 7 and 8) which sometimes open into the invaginations of the plasma membrane (Fig. 8). At the posterior face deep surface invaginations, much wider than at the anterior face, are seen. The many irregularly shaped 'vacuoles' are apparently in connection with the surface invaginations indicated by the presence of a coating material found in the 'vacuoles' and at the outside of the cell surface of the posterior face (Fig. 6). This material is also present at the anterior face (Fig. 7). There are many cytoplasmic organelles at the posterior

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Figs. 1–4. *Pollimyrus isidori*, 12 mm, 32 days old.

Fig. 1. Schematic representation of maximal extent (dorsal–ventral, rostral–caudal) of larval electric organ (LO). The electrocytes of this organ are found over the whole length of the deep lateral muscle (see Fig. 4). The body cavity (BC) considerably limits the ventral part of the LO. In the caudal peduncle the electrocytes of the typical mormyrid electric organ (= adult electric organ) are found.

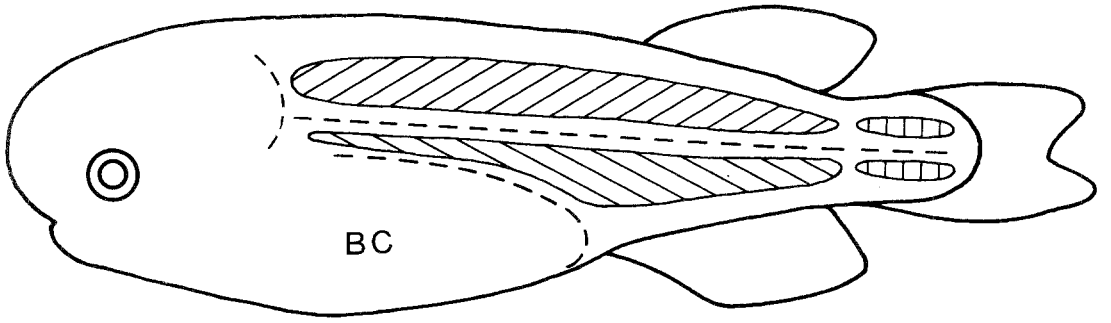
Figs. 2–4. Light micrographs, Azan stain.

Fig. 2. Sagittal section showing rows of larval electrocytes in the caudal region (small arrows) and the most rostral ones (large arrows). Level of cross-section of Fig. 4 and the areas enlarged in Figs. 3 and 17 are indicated.

Fig. 3. Rows of larval electrocytes with long stalks (arrows). 'Normal' muscle fibres (M) can be seen below the electrocytes (E). The myotomic segmentation is still evident. The myoseptum is replaced by a large quantity of loose connective tissue (see also Fig. 4) at the level of the electrocytes.

Fig. 4. Cross-section (see Fig. 2) showing the four parts of the LO. The limits (dotted lines) are only approximate because of intermediate stages between muscle fibres and electrocytes.

The horizontal myoseptum and muscle fibres limit the two dorsal from the two ventral parts of the organ in the horizontal plane. Connective tissue and the skeletal elements constitute the medial separation.

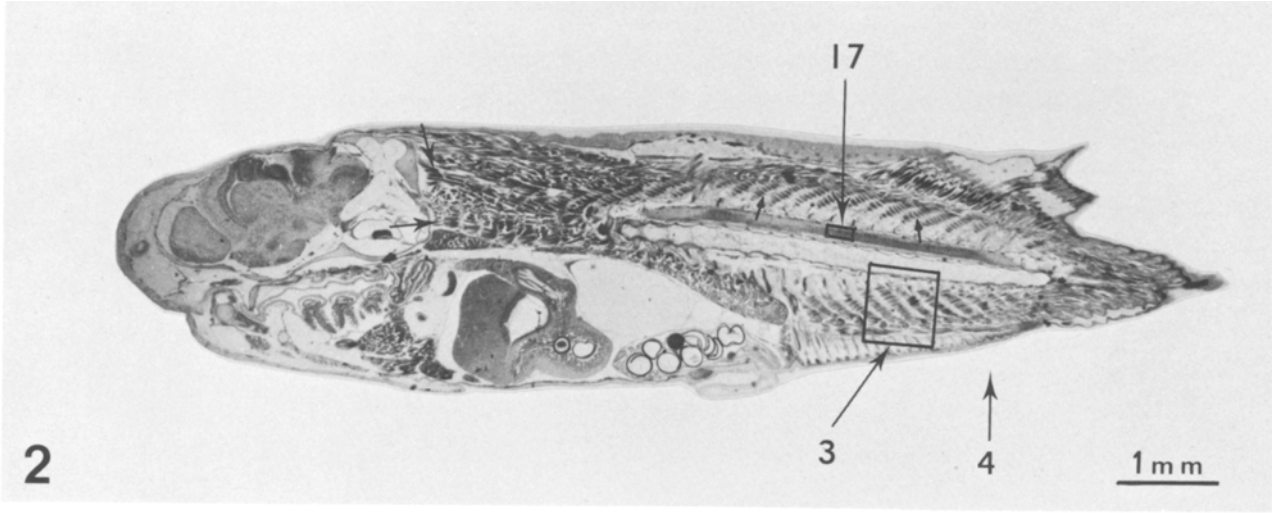


Larval Electric Organ

Adult Electric Organ

1

1mm



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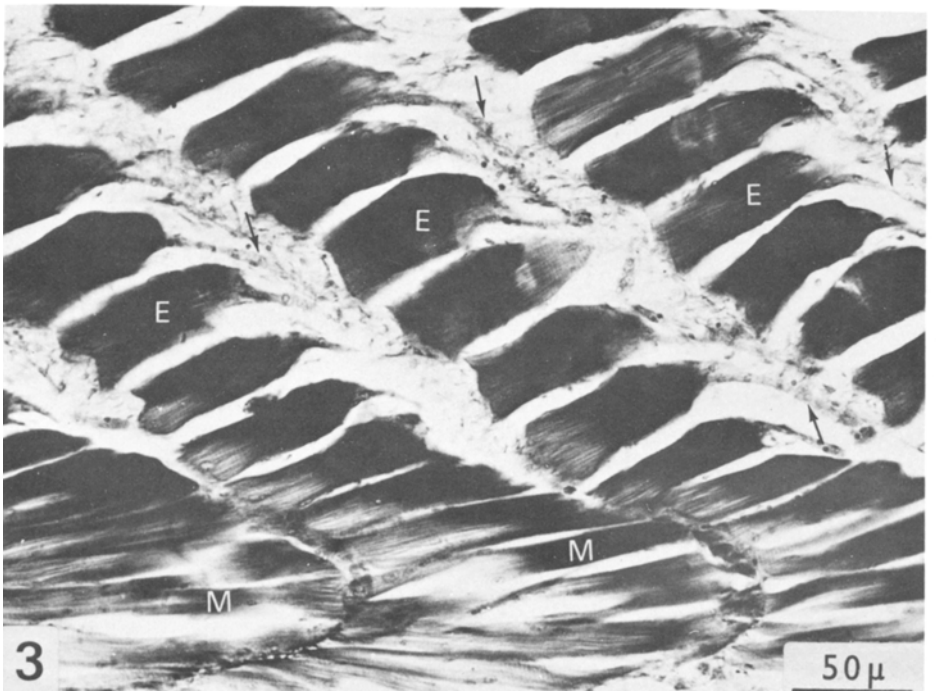

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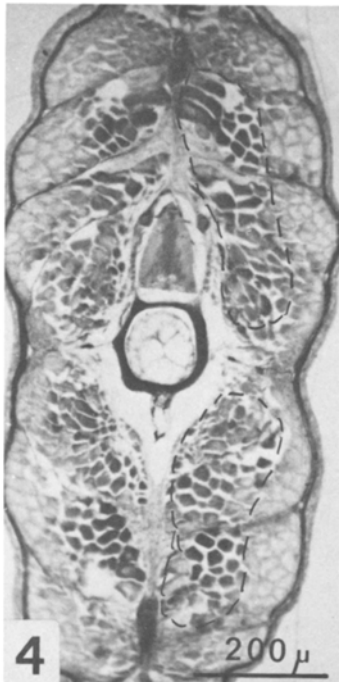

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face: groups of pleiomorphic nuclei, Golgi apparatus, oblong mitochondria and multivesicular bodies.

In the central part of the electrocyte, myofibrils can be seen (Fig. 11) which are similar to those found in muscle fibres (Fig. 10). However, in the electrocyte the bundles of myofibrils are arranged orthogonally (Fig. 11), whereas in muscle fibres the myofibrils run always in one direction. The striations of the myofibrils in the electrocytes are easily visible, but less clear than in the muscle fibres. The Z line is clearly visible (Figs. 11 and 14) whereas the H zone is only just perceptible. Smooth endoplasmic reticulum is found in electrocytes as well as in muscle fibres.

The stalk of the electrocyte originates at the posterior face (Figs. 3 and 5). It contains nuclei, mitochondria and shows the same type of surface invaginations found at the posterior face. The myofibrils do not extend into the stalk (Fig. 14).

Innervation of the distal ends of the stalks

Light microscopic observations show that the electrocyte stalks described above receive the innervation (Figs. 5, 12 and 13). Only the distal portion of the stalk is innervated and it is wider than the proximal part (Fig. 12). The myelin sheath terminates at the level of the synaptic terminal (Fig. 13). These terminals show the typical structure of synapses of electrocytes with a synaptic cleft about 70 nm wide and many synaptic vesicles near the presynaptic membrane (Figs. 15 and 16).

Free cells

The stalks extend into the space filled with loose connective tissue which separates the rows of electrocytes (Fig. 3). Next to the stalks free cells are found (Fig. 5), which contain many cytoplasmic organelles and a large nucleus (Fig. 9).

Electromotorneurones

It has been shown above that the stalk of the larval electrocyte receives the innervation, but this result gives no information about the location of the

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Figs. 5–11. *Pollimyrus isidori*, 12 mm, 32 days old.

Fig. 5. Light micrograph showing a series of regularly arranged electrocytes. Toluidine blue stained 1 μm section. Note the stalks (arrows) on the posterior face (P). Free cells indicated by double arrows. A, anterior face, m, muscle fibre.

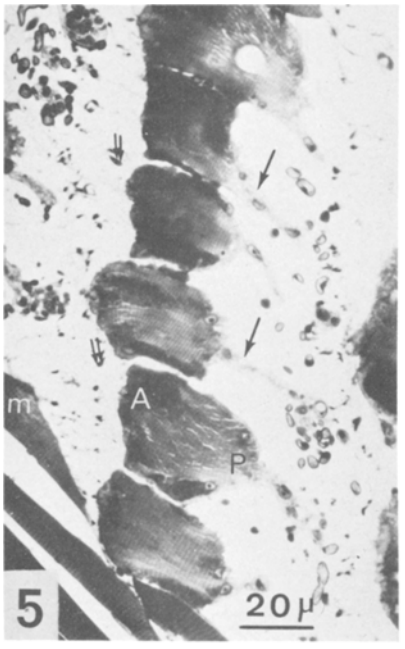
Figs. 6–11. Electron micrographs.

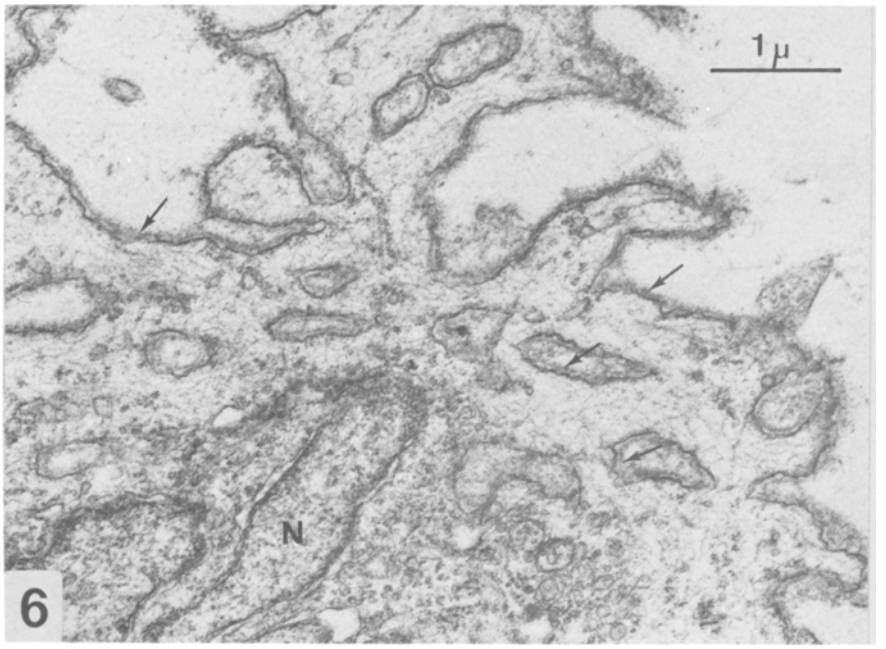
Fig. 6. Detail of the posterior face (P in Fig. 5). Note the invaginated nuclei (N). The plasma membrane and the interior of the numerous vacuoles are covered by a thick, coating substance (arrows).

Figs. 7 and 8. Detail of the anterior face (A in Fig. 5). The cytoplasm is full of vesicles (single arrows) which sometimes open (arrow in Fig. 8) into the invaginations (double arrow) or vacuoles.

Fig. 9. Detail of a free cell. Note the numerous cytoplasmic organelles. N, nucleus, r, granular endoplasmic reticulum, g, Golgi apparatus, m, mitochondrion.

Figs. 10 and 11. Difference between parallel orientation of myofibrils of normal muscle fibre (Fig. 10) and orthogonal arrangement of two bundles of myofibrils in an electrocyte (Fig. 11).


m
A
P
5
20μ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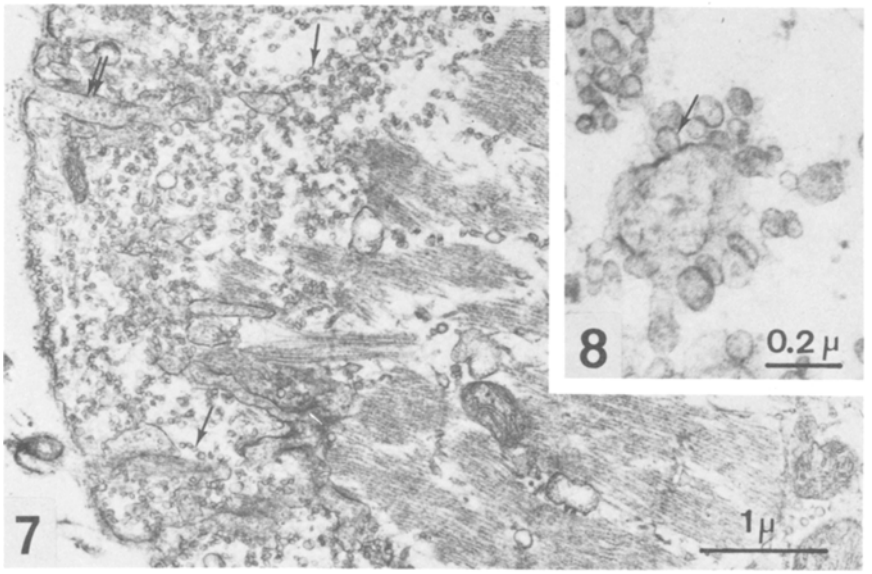
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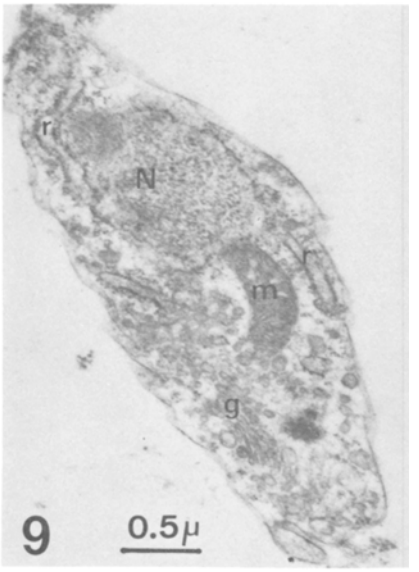
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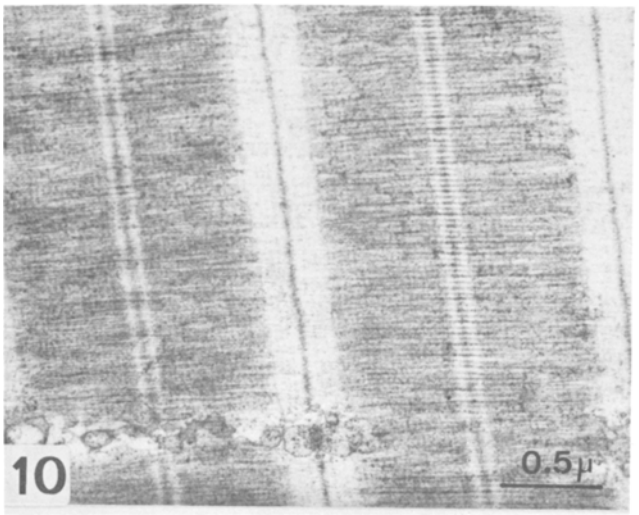
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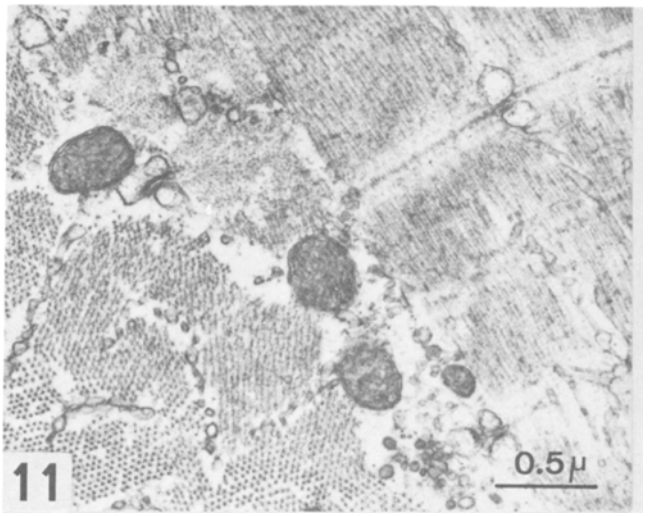
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0.5μ

innervating neurones. In the spinal cord rows of giant neurones can be found (Figs. 17 and 18) extending over nearly the whole length of the larval electric organ and they are lacking only in the most rostral part of the spinal cord and in the caudal region of the larval electric organ. The axons of these cells leave the spinal cord by the ventral roots and then run in dorsal and ventral directions presumably to innervate the electrocytes in a way similar to the innervation of the electrocytes of the adult organ of mormyrids (Szabo, 1957a) and that of *Gymnarchus* (Dahlgren, 1914). We believe these cells to be the electromotorneurones of the larval electric organ. They appear for the first time in 6 day old fish, two days before the first discharge, and they disappear at the time when the larval electric organ degenerates (Kirschbaum, in preparation).

Histochemistry of acetylcholinesterase

The histochemical investigations reveal a strong acetylcholinesterase activity not only at the innervated stalk, but also a strong activity at the anterior face of the electrocyte (Fig. 19).

Electrophysiology of the larval electric organ

The anatomical, histological and cytological description of the larval electric organ was completed by a parallel ontogenetic study of the larval electric organ discharge (L.EOD), its emergence, development and disappearance and the appearance and development of the adult electric organ discharge (A.EOD). These data are presented in full detail elsewhere (Westby and Kirschbaum, 1977a,b) but a brief description of the time course of the development will be presented here.

Fig. 21 shows the results of a study in which a peer group of six *Pollimyrus* were continuously monitored from hatching to adulthood. At 27° C the first L.EODs are detected at 8 days from spawning when the fish are immobile and still possess their yolk sacs. The L.EOD is *head-positive* and approximately 1 millisecond in duration

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Figs. 12–16. *Pollimyrus isidori*, 12 mm, 32 days old. Innervation of the larval electrocyte. **Figs. 12 and 13**, light micrographs; **Figs. 14–16**, electron micrographs.

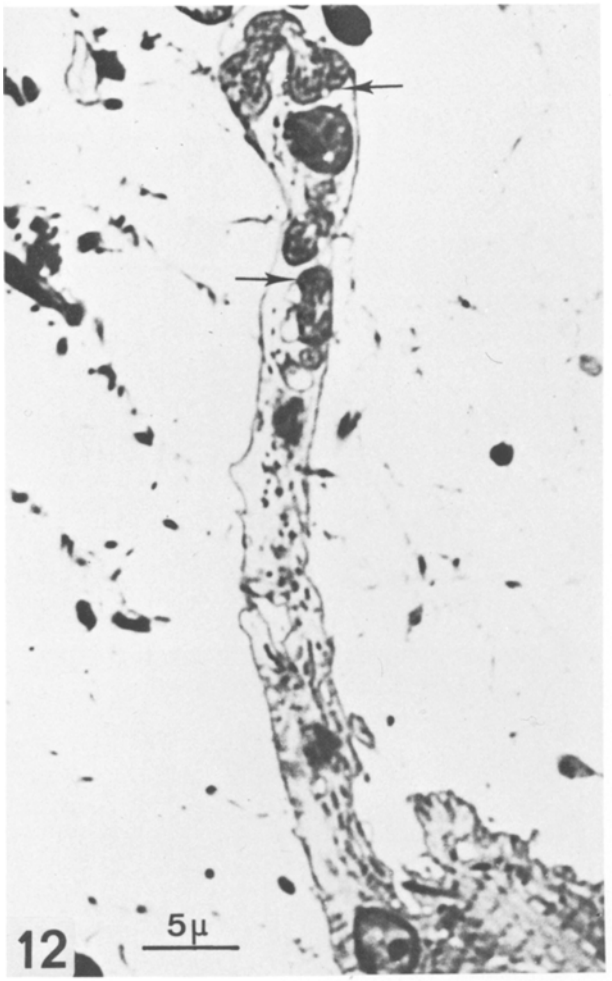
Fig. 12. Longitudinal section of the stalk. Note the nerve terminals (arrows) at the distal end. Toluidine blue stain.

Fig. 13. Transverse section at the tip of the stalk with nerve terminals (arrows). The strongly stained myelin sheath terminates at the level of the synaptic terminal (see small arrows). Toluidine blue stain.

Fig. 14. Longitudinal section at the base of the stalk (see Fig. 5). Note the abundance of plasma membrane invaginations and the numerous vacuoles in the cytoplasm of the stalk (arrows) (see also Fig. 6). The regularly arranged myofibrils are almost absent in the stalk.

Fig. 15. Distal end of stalk with nerve terminals. Synaptic contacts (between arrows) are indicated. N, nerve, E, electrocyte.

Fig. 16. Detail of a nerve terminal. Accumulation of synaptic vesicles (small arrows) between the mitochondria (m) and the presynaptic membrane (Pr). The active sites, thickened areas of the membrane are indicated by large arrows. Ps, postsynaptic membrane.



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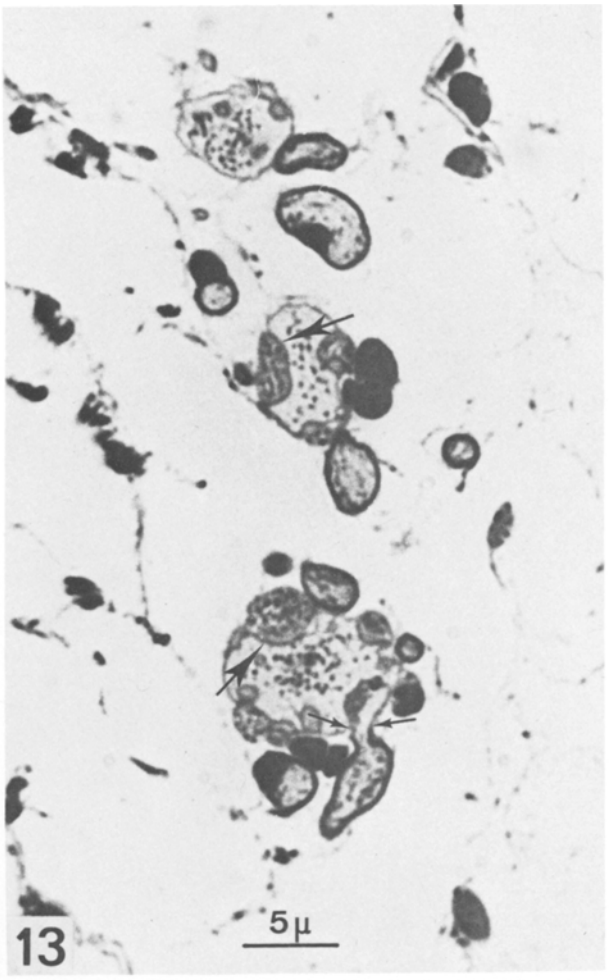

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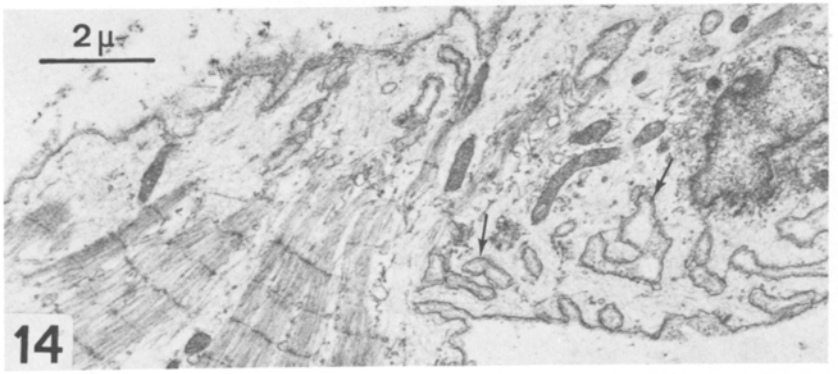

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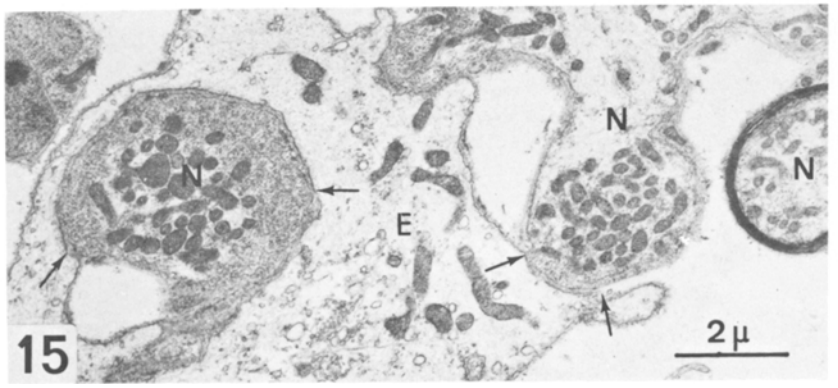

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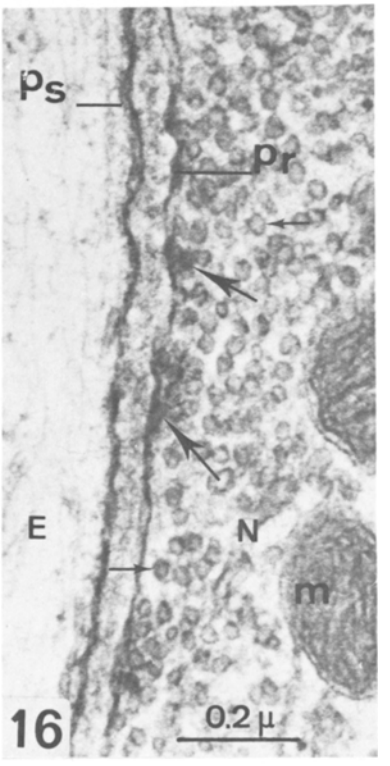

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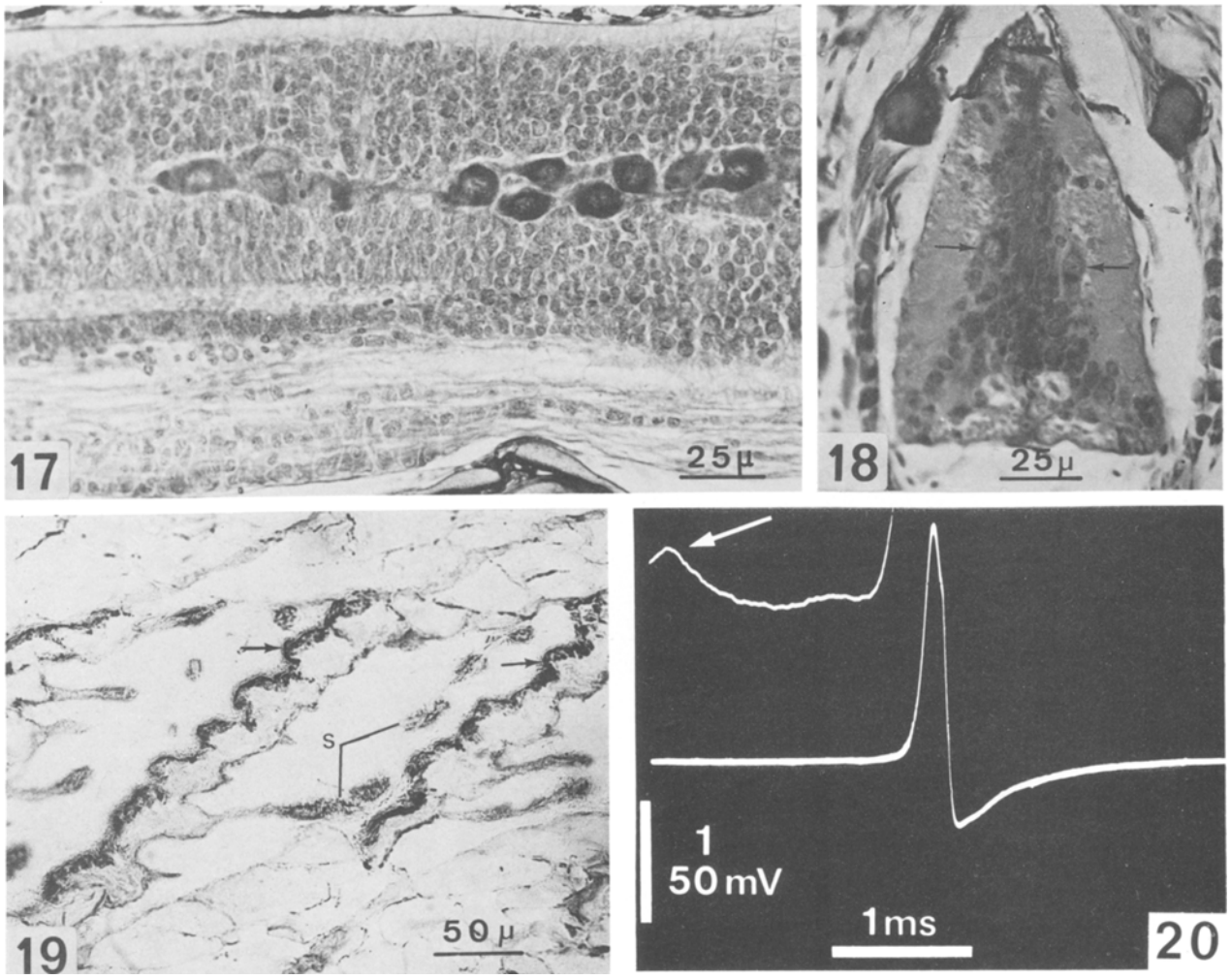

Figs. 17, 18 and 20. *Pollimyrus isidori*, 12 mm, 32 days old. **Fig. 19.** *Pollimyrus isidori*, 18 mm, 72 days old.

Figs. 17–19. Light micrographs.

Fig. 17. Sagittal section of spinal cord (see Fig. 2) showing large neurones, probably the electromotoneurones of the larval electrocytes. Azan stain.

Fig. 18. Enlarged area of spinal cord in Fig. 4 showing the position (arrows) of the large neurones (see Fig. 17). Azan stain.

Fig. 19. AChE activity in sagittally sectioned electrocytes. Note the strong activity localized on the stalks (s) and the anterior faces (arrows).

Fig. 20. Oscilloscope recording of the larval electric discharge as seen at the output of the recording cell (see Methods). Head positivity upwards. Lower trace: the main head positive discharge. bar, 50 mV. Upper trace: high gain simultaneous recording showing the characteristic preceding phase (arrow) used to trigger the sweep. bar, 1 mV; bar, 1 millisecond.

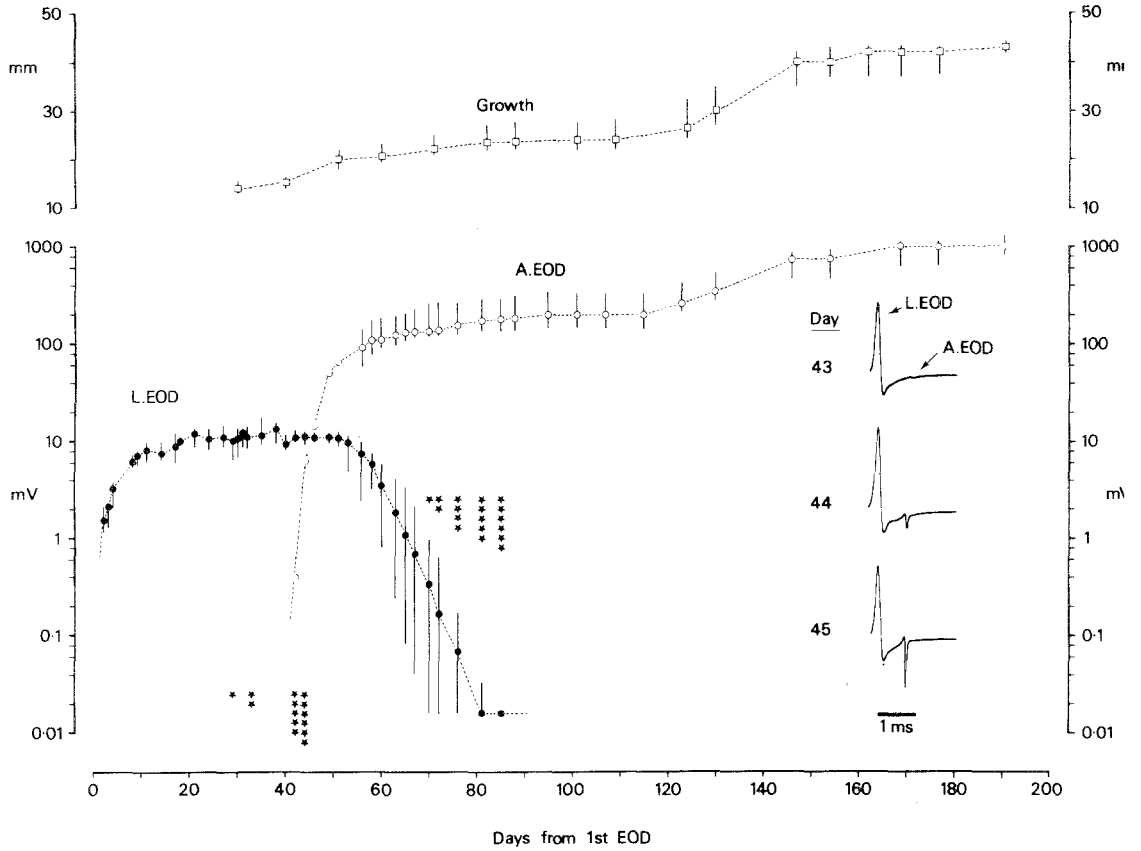

Fig. 21. Electric organ discharge (EOD) amplitude and growth curves for a peer group of six *Pollimyrus* larvae continuously monitored from hatching to adulthood. Mortality reduced the number of animals to four by Day 200. Ordinate: EOD amplitude in mV. Abscissa: Days from first EOD – add 8 for time of spawning. Filled circles and vertical bars represent the median and range of the larval (L.)EOD amplitude as measured with a 10 ml recording cell. Open circles and vertical bars show the median and range of the adult (A.)EOD starting on the day when the whole group possesses the A.EOD. Medians only are given for the first three days due to the variation in time of onset of the A.EOD. Asterisks at around 40 days on the abscissa show the number of animals with the first detectable sign of the A.EOD while those around 80 days represent the number of fish with completely reduced L.EOD. The growth curve shows the median and range for the overall lengths of the fish. Note that the A.EOD amplitudes follow the growth curve very closely. Bottom right inset shows oscilloscope records of the appearance of the A.EOD in one of the fish on three successive days.

(Fig. 20) whereas the adult discharge is very brief (50 microseconds) and head-negative. The L.EOD amplitude rapidly increases to reach a plateau amplitude at about 20 days from the first EOD. The first A.EODs are seen in fish about 40 days from their first discharges. The insert in Fig. 21 shows how the A.EOD first appears as a slight inflexion in the baseline 700 microseconds after each L.EOD. Its

amplitude soon surpasses that of the L.EOD and rises to ten times the size of the larval pulse within 10 days. The two discharges co-exist for a period of about 40 days and the A.EOD amplitude continues to increase throughout the development of the animal. The growth curve for the fish (Fig. 21) shows that the rate of amplitude increase is closely related to the growth of the animals.

The discharge frequency shows a very rapid increase from the initial rate. The mean EOD interval was 3 min during the first hour falling to 7 seconds in the sixth hour. All fish were discharging within the adult range of frequencies within 24 h although the highest burst frequencies did not appear until 10 days from the first EOD (Westby and Kirschbaum, 1977a). No discontinuity was seen to be associated with the appearance of the A.EOD or the disappearance of the L.EOD thus suggesting that a common pacemaker controls both organs.

Discussion

GENERAL FEATURES OF THE LARVAL ELECTRIC ORGAN OF *POLLIMYRUS*

Electric organs, despite their convergent development in different taxonomic groups, display two major general features (Fessard, 1958; Bennett, 1971): the functional elements, the electrocytes, show a high degree of spatial organization; they are aligned in series and in parallel either in the longitudinal or the dorso–ventral axis of the fish; the two faces (innervated and noninnervated face) show considerable surface invaginations; and myofibrils are found to a variable degree in the cytoplasm.

Arrangement of electrocytes

The electrocytes of *Pollimyrus* are arranged in parallel in each myotome but at about 45° to the longitudinal axis of the fish. There is loose connective tissue between the rows, but no walled tube of connective tissue around the electrocytes. All these features point to the very primitive state of this organ, almost comparable to the electric organs of certain skates (Ewart, 1888, 1892).

Invaginations of the plasma membrane

The large amount of surface invagination of the anterior and posterior faces of the electrocytes of *Pollimyrus* is comparable to that found in the electrocytes of strongly as well as of weakly electric fish (Luft, 1956, 1957, 1958; Mathewson *et al.*, 1958, 1961; Wachtel *et al.*, 1961; Waxman *et al.*, 1972; Srivastava and Baillet-Derbin, 1973; Schwartz *et al.*, 1975; Machado *et al.*, 1976).

In *Pollimyrus* the non-innervated face with its linear invaginations and vesicles is slightly more complex than the posterior, innervated face. The surface invaginations of the innervated face, however, seem to be more pronounced than those of the anterior face, thereby leading to an increase in surface area of the posterior face. A similar difference in surface invaginations between the two electrocyte faces can be found in *Electrophorus, Torpedo*, the mormyrids and the gymnotids. The coating

material covering the exterior both of the anterior and posterior faces of the electrocyte has also been found in other species of electric fish (Schwartz *et al.*, 1975; Machado *et al.*, 1976).

The origin of the electrocytes

The electrocytes of the *Pollimyrus* larval electric organ are very similar to muscle fibres and only slightly shorter and thicker than these cells. In the cytoplasm, bundles of myofibrils with clearly visible Z lines and discernible H zones are found which leave no doubt about the myogenic origin of these cells. The muscular origin of electrocytes in electric fish has been demonstrated by ontogenetic (Ewart, 1892; Ogneff, 1898; Dahlgren, 1914; White, 1918; Johnels, 1956; Szabo, 1960, 1961a, 1966; Keynes, 1961; Srivastava and Szabo, 1972; Kirschbaum, 1977), and cytological studies (Engelmann, 1894; Wachtel, 1964; Bruns, 1971; Schwartz *et al.*, 1975; and others). Westby and Kirschbaum (1977a) have shown that the larval electric organ activity, early during ontogeny is very often associated with movements, which is a further argument for the muscular origin of the electrocytes of *Pollimyrus*.

Innervation

As described above the electrocytes possess long stalks on their posterior faces. The nerve terminals are found at its distal end. Similar stalked electrocytes have been described in other mormyrids, *Malapterurus* and *Steatogenys*. The synapses between the electromotor nerve and the electrocyte show the same characteristics as those described in other electric fish (Srivastava and Baillet-Derbin, 1973; Schwartz *et al.*, 1975; Machado *et al.*, 1976, and others). The terminal is well embedded in the surface of the innervated face of the electrocyte. The pre- and postsynaptic membranes are separated by a space of about 70 nm within which an electron-dense substance is clearly visible. This material appears to be continuous with the coating material found over the rest of the surface. The terminal region of the axon is characterized by the presence of relatively small mitochondria and cluster of synaptic vesicles closely associated with the presynaptic membrane.

The agglomeration of giant neurons, which was found in the spinal cord over nearly the whole length of the larval electric organ, is believed to be the electromotorneurones of the larval electrocytes. These cells have a shape similar to the electromotorneurones of the adult organ of mormyrids which are found in the caudal peduncle (Szabo, 1957a, 1961b) and in the 12 mm *Pollimyrus* described here, these neurones even have the same size as the electromotorneurones found simultaneously in the caudal peduncle (Kirschbaum, in preparation). It has already been shown that the electromotorneurones are the largest nerve cells to be found in the spinal cord (Fessard, 1958; Bennett, 1971). The distribution of these cells over nearly the whole length of the larval electric organ of *Pollimyrus* is very similar to the distribution of electromotorneurones in the spinal cord of *Gymnarchus*

(Dahlgren, 1914), where these cells also extend over the whole length of the electric organ.

TWO DISTINCT ELECTRIC ORGANS EXIST SIMULTANEOUSLY IN *POLLIMYRUS*

The larval electric organ of *Pollimyrus* is found in the deep lateral muscle rostral to the caudal peduncle. It is functional very early during ontogeny (Kirschbaum and Westby, 1975, Westby and Kirschbaum, 1977a) and is completely reduced in 84 day old fish (26.5 mm total length) (Kirschbaum, in preparation). The electrocytes of the well-known electric organ of mormyrids (Fessard, 1958; Bennett, 1971) are present in the caudal peduncle caudal to the larval electric organ (Fig. 1). We have termed this organ, in contrast to the larval organ, the adult electric organ because it persists in adult fish. Ontogenetic studies have shown (Szabo, 1960, 1961a; Kirschbaum, in preparation) that the adult organ develops rather late during ontogeny and that it is functional only when it is well developed (Westby and Kirschbaum, 1977b). In 48 day old *Pollimyrus* (15–15½ mm long) both organs, the larval and the adult electric organ, are functional (Westby and Kirschbaum, 1977b). This stage persists for several weeks, until the larval electric organ has been fully reduced. This is the first example of two distinct electric organs, corresponding to two distinct evolutionary steps in the development of electric organs, existing simultaneously in one species.

Both organs originate in the deep lateral muscle (Kirschbaum, 1977) and thus can be called homologous structures. The adult organ is, however, much more complex and no doubt evolved later in the caudal peduncle. The electrocytes of both organs still have several features in common: they are stalked electrocytes, at the tip of which the nerve terminals are found. The surface invaginations of the innervated face are slightly wider than those at the non-innervated face. A strong AChE activity is found at the anterior face of the larval and of the adult electric organ (Tsuji, unpublished data) of *Pollimyrus* as well as at the anterior face of the adult electric organ of *Gnathonemus* (Tsuji, 1976; Tsuji and Verma, 1977), another mormyrid fish. Well-organised myofibrils could be found in the cytoplasm of the electrocytes of both organs. The main differences in the two types of electrocytes in *Pollimyrus* are their size – the differentiated electrocytes of the adult organ are large cells which no longer resemble muscle fibres – and their physiological properties. The striking differences in polarity, form and amplitude of larval and adult discharges of *Pollimyrus* can probably be explained in terms of the membrane properties of their respective electrocytes and the gross morphological differences both in their form and spatial arrangement in the two electric organs. Since the electrocytes of both organs are innervated by stalks on their posterior faces the polarity difference could be directly due to a relative inexcitability of the anterior membranes of the larval electrocytes. However another explanation might be that the unusual columnar arrangement of the larval organ (the dorsal and ventral pairs of columns are at 90° to each other), the loose packing of the electrocytes within the

columns, and their elongate form, do not constitute an electric organ with the necessary electrical properties for the efficient channelling of current required to depolarize the anterior electrocyte faces. Furthermore there is no evidence for the connective tissue barriers to local current flow seen in the adult electric organ (Schwartz *et al.*, 1975; Bell *et al.*, 1976) which might also explain the unexpectedly low voltage output of the larval organ compared with the adult structure in the caudal peduncle (Fig. 21), even though the total number of electrocytes in each organ is similar. Further studies will show if a larval electric organ, similar to that described for *Pollimyrus*, can also be found in other mormyrid fishes. Heymer and Harder (1975) showed that the discharge of a larva of the mormyrid *Stomatorhinus* is different from the adult discharge, which suggests that a larval electric organ also exists in this species.

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References

BELL, C. C., BRADBURY, J. and RUSSELL, C. J. (1976) The electric organ of a mormyrid as a current and voltage source. *Journal of Comparative Physiology* **110**, 65–88.

BENNETT, M. V. L. (1971) Electric organs. In: *Fish Physiology* 5, (edited by HOAR, W. S. and RANDALL, D. J.), pp. 347–491. New York and London: Academic Press.

BRUNS, V. (1971) Elektrisches Organ von *Gnathonemus* (Mormyridae). Elektrische Platte und Innervation. *Zeitschrift für Zellforschung und mikroskopische Anatomie* **122**, 538–63.

DAHLGREN, U. (1910) Origin of electricity tissues in fishes. *American Naturalist* 44, 193–202.

DAHLGREN, U. (1914) Origin of the electric tissues of *Gymnarchus niloticus. Papers from the Tortugas Laboratory*, Carnegie Institute of Washington, 6, 159–203.

ENGELMANN, T. W. (1894) Die Blätterschicht der elektrischen Organe von *Raja* in ihren genetischen Beziehungen zur quergestreiften Muskelsubstanz. *Archiv für die gesamte Physiologie* **57**, 149–80.

EWART, J. C. (1888) The electric organ of the skate. On the development of the electric organ of *Raja batis*. *Philosophical Transactions of the Royal Society of London*, Series **B**, **179**, 399–416.

EWART, J. C. (1892) Observations on the structure, relations, progressive development, and growth of the electric organ of the skate. *Philosophical Transactions of the Royal Society of London*, Series **B 183**, 389–420.

FESSARD, A. (1958) Les organes électriques. In: *Traité de Zoologie XIII* (edited by GRASSÉ, P. P.), pp. 1143–238. Paris: Masson et Cie.

HEYMER, A. and HARDER, W. (1975) Erstes Auftreten der elektrischen Entladungen bei einem jungen Mormyriden. *Naturwissenschaften* **62**, 489.

JOHNELS, A. G. (1956) On the origin of the electric organ in *Malapterurus electricus. Quarterly Journal of Microscopical Science* **97**, 455–64.

KEYNES, R. D. (1961) The development of the electric organ in *Electrophorus electricus* L. In: *Bioelectrogenesis* (edited by CHAGAS, C. and DE CARVALHO, A. P.) pp. 14–19. Amsterdam: Elsevier.

KIRSCHBAUM, F. (1975) Environmental factors control the periodical reproduction of tropical electric fish. *Experientia* **31**, 1159–60.

KIRSCHBAUM, F. (1977) Electric organ ontogeny: Distinct larval organ precedes the adult organ in weakly electric fish. *Naturwissenschaften* **64**, 387–8.

KIRSCHBAUM, F. and WESTBY, G. W. M. (1975) Development of the electric discharge in Mormyrid and Gymnotid fish (*Marcusenius sp.* and *Eigenmannia virescens*) *Experientia* **31**, 1290–3.

LUFT, J. H. (1956) The fine structure of the electric organ of the electric eel and torpedo ray. *Journal of Biophysical and Biochemical Cytology* **2**, Suppl. 229–32.

LUFT, J. H. (1957) The histology and cytology of the electric organ of the electric eel. (*Electrophorus electricus* L.) *Journal of Morphology* **100**, 113–39.

LUFT, J. H. (1958) The fine structure of electric tissues. *Experimental Cell Research Suppl.* **5**, 168–82.

MACHADO, R. D., DE SOUZA, W., COTTA-PEREIRA, G. and OLIVEIRA-CASTRO, G. (1976) On the fine structure of the electrocyte of *Electrophorus electricus* L. *Cell and Tissue Research* **174**, 355–66.

MATHEWSON, R., MAURO, A., AMATNIEK, E. and GRUNDFEST, H. (1958) Morphology of main and accessory electric organs of *Narcine brasiliensis* (Olfers) and some correlations with their electrophysiological properties. *Biological Bulletin* **115**, 126–35.

MATHEWSON, R., WACHTEL, A. and GRUNDFEST, H. (1961) Fine structure of electroplaques. In: *Bioelectrogenesis* (edited by CHAGAS, C. and DE CARVALHO, A. P.), pp. 25–53. Amsterdam: Elsevier.

OGNEFF, J. (1898) Einige Bemerkungen über den Bau des schwachen elektrischen Organs bei den Mormyriden. *Zeitschrift für wissenschaftliche Zoologie* **64**, 565–95.

REYNOLDS, E. S. (1963) The use of lead citrate at high pH as an electron opaque stain in electron microscopy. *Journal of Cell Biology* **17**, 208–12.

SCHLICHTER, H. (1906) Über den feineren Bau des schwach elektrischen Organs von *Mormyrus oxyrhynchus*. *Zeitschrift für wissenschaftliche Zoologie* **84**, 479–525.

SCHWARTZ, I. R., PAPPAS, G. D. and BENNETT, M. V. L. (1975) The fine structure of electrocytes in weakly electric teleosts. *Journal of Neurocytology* **4**, 87–114.

SZABO, T. (1957a) *Anatomo-physiologie comparée des divers organes électriques et de leurs centres nerveux de commande.* Paris: Thèse.

SZABO, T. (1957b) Le muscle d'origine de l'organe électrique d'un mormyre. *Zeitschrift für Zellforschung und mikroskopische Anatomie* **47**, 77–9.

SZABO, T. (1960) Development of electric organ of Mormyridae. *Nature* **188**, 760–2.

SZABO, T. (1961a) Rapports ontogénétiques entre l'organe électrique, son innervation et sa commande encéphalique (*Mormyrus rume*). *Zeitschrift für Zellforschung und mikroskopische Anatomie* **55**, 200–3.

SZABO, T. (1961b) Anatomo-physiologie des centres nerveux spécifiques de quelques organes électriques. In: *Bioelectrogenesis* (edited by CHAGAS, C. and DE CARVALHO, A. P.) pp. 185–201. Amsterdam: Elsevier.

SZABO, T. (1966) The origin of electric organs of *Electrophorus electricus*. *Anatomical Record* **155**, 103–10.

SRIVASTAVA, C. B. L. and SZABO, T. (1972) Development of electric organs of *Gymnarchus niloticus* (Fam. Gymnarchidae). I. Origin and histogenesis of electroplates. *Journal of Morphology* **138**, 375–85.

SRIVASTAVA, C. B. L. and BAILLET-DERBIN, C. (1973) Etude ultrastructurale de l'organe électrique d'un poisson électrique à faible décharge: *Eigemannia virescens*. *Comptes rendus de l'Académie des Sciences, Paris* **277**, 2209–12.

TAVERNE, L. (1971) Note sur la systématique des poissons Mormyriformes. Le problème des genres *Gnathonemus Gill, Marcusenius Gill, Hippopotamyrus Pappenheim, Cyphomysus Myers* et les nouveaux genres *Pollimyrus* et *Brienomyrus. Revue Zoologique et Botanique Africaine* **LXXXIV**, 99–110.

TSUJI, S. (1974) On the chemical basis of thiocholine methods for demonstration of acetylcholinesterase activities. *Histochemistry* **42**, 99–110.

TSUJI, S. (1976) Acetylcholinesterase activity not associated with innervation in the pedicled electroplaque of Mormyrid fishes. *Journal of Neurochemistry* **26**, 191–2.

TSUJI, S. and VERMA, V. (1977) Synaptic and non-synaptic actetylcholinesterase activity in the electroplaque of Mormyrid fish. *Journal of Neurocytology*, **6**, 119–23.

WACHTEL, A. (1964) The ultrastructural relationships of electric organs and muscle. I. Filamentous systems. *Journal of Morphology* **114**, 325–59.

WACHTEL, A., MATHEWSON, R. and GRUNDFEST, H. (1961) Electron microscopic and histochemical comparison of the two types of electroplaques of *Narcine brasiliensis. Journal of Biophysical and Biochemical Cytology* **11**, 663–675.

WAXMAN, S. G., PAPPAS, G. D. and BENNETT, M. V. L. (1972) Morphological correlates of functional differentiation of nodes of Ranvier along single fibres in the neurogenic electric organ of the knife fish *Sternarchus. Journal of Cell Biology* **53**, 210–24.

WESTBY, G. W. M. and KIRSCHBAUM, F. (1977a) Emergence and development of the electric organ discharge in the mormyrid fish *Pollimyrus*. I. The larval discharge. *Journal of Comparative Physiology* in press.

WESTBY, G. W. M. and KIRSCHBAUM, F. (1977b) Emergence and development of the electric organ discharge in the mormyrid fish *Pollimyrus*. II. The appearance and development of the adult discharge. *Journal of Comparative Physiology*, submitted.

WHITE, E. G. (1918) The origin of the electric organs in *Astroscopus guttatus. Papers from the Tortugas Laboratory*, Carnegie Institute of Washington **12**, 141–72.