"Note on the Electromotive Force of the Organ Shock and the Electrical Resistance of the Organ in *Malapterurus electricus*."

By Francis Gotch, M.A., F.R.S., and G. J. Burch, M.A. Oxon. Received July 18,—Read November 16, 1899.

(From the Physiological Laboratory, Oxford.)

Electrometer Records of the Organ Shock.

In the month of March of the present year, 1899, the Committee of the Corporation Museum, Liverpool, kindly placed at the disposal of one of us (F. G.) two living specimens of *Malapterurus electricus*. They were exhibited at a lecture delivered in London at the Royal Institution on March 17. One of the fish died from accidental injury, the other was employed by us for the purpose of determining the electromotive force of the organ shock, and for investigating such other points of interest as were feasible.

We decided to employ for the determinations the special capillary electrometer made by one of us (G. J. B.), which we had utilised in our researches upon the electrical phenomena of nerve.* Our previous work upon the organ of *Malapterurus* rendered it certain that considerable precautions would have to be adopted in connection with this instrument, since it was a much more sensitive one than those we had used in the researches described in our previous paper upon the subject.† It was therefore first necessary to make a number of preliminary experiments in order to reduce the extent of any excursion due to the organ shock within such limits that it could be recorded. Several trials with different voltages resulted in our employing a non-inductive shunt of three incandescent lamps; these were placed in parallel between the electrometer connections and had a combined resistance of 26·6 ohms. We diminished the size of the record still further by replacing the high objective of the projecting microscope by a lower power, Zeiss, B.

Our previous experiments made in 1895 showed us that the organ shock developed so rapidly that the records then obtained were all too steep to admit of accurate analysis. It seemed certain, therefore, that the recorded curves, due to the rise and fall of the meniscus, would have to be of a more prolonged type in order that the rate of development of the electromotive force of the shock might be deduced from their analysis.

In the hope of obtaining curves of a sufficiently prolonged character, both the physical and the physiological conditions of experiment were

* 'Roy. Soc. Proc.,' vol. 63, p. 300, 1898.

† 'Phil. Trans.,' B, vol. 187 (1896), p. 347.

modified; the rate of transit of the photographic plate upon which the image of the mercurial meniscus was projected, was made much quicker, whilst the whole organ of the fish was effectually cooled to a low temperature, 5° C.

As we had only one fish, we made several attempts to catch a record of the natural discharge of the organ upon the travelling plate. It was found, however, to be practically impossible to do this, since the reflex responses obtained from the uninjured fish were not merely uncertain as to their time of commencement but also very variable as to their intensity.

We determined, therefore, to kill the fish and utilise the nerve organ preparation for the purpose of obtaining the necessary data.

A further consideration induced us to take this course. Determinations made upon an entire fish must be of little value for the calculation of the E.M.F. of the change produced in each excited disc, owing to the complicated physical conditions of an experiment made under these circumstances. On the other hand it appeared to be easy to cut an organ strip and arrange it so that the distance between the contacts, which connected it with the electrometer, should be perfectly definite; moreover, with such a strip the number of discs comprised in the actual distance between the contacts could be enumerated after the experiment by examining appropriate sections made through the whole of this portion of the organ.

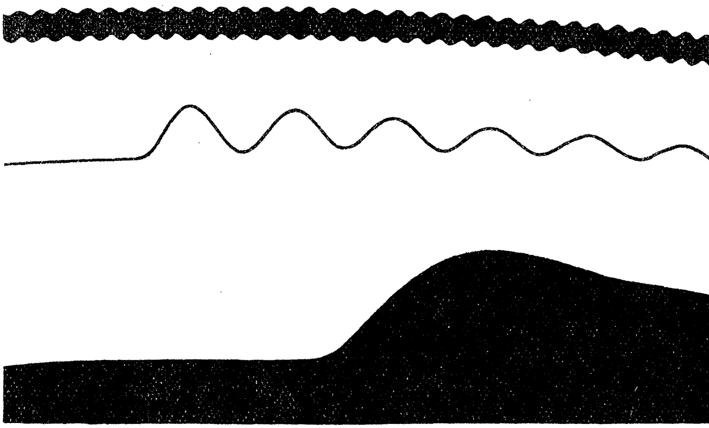
The fish was therefore anæsthetised by immersion in ice-cold water and then killed. A strip of the organ was now detached and the nerve carefully dissected out; this nerve organ preparation was placed upon a glass plate in a special moist chamber kept at a uniform temperature of 5° C. The nerve was excited by a single break induced current of such an intensity as our previous experience had shown to be necessary in order to evoke a maximal organ response (Kronecker coil with core, one Daniell in primary, secondary at 10,000). The break induction shock was produced by the movement of the recording pendulum, and was so timed as to occur when the photographic plate carried by the pendulum reached the slit upon which the image of the meniscus was projected. The electrometer contacts were so placed as to lie 15 mm. apart upon the thickest portion of the organ. Thirteen photographs were taken, of which two (Nos. 3012, 3013) gave excellent records suitable for accurate analysis. In the first of these (3012), a facsimile reproduction of which is shown in fig. 1, the three-lamp shunt was placed between the electrometer terminals. In the second record (3013) the two-lamp shunt was employed.

The response in both these experiments was very marked, and, owing probably to the low temperature, was more delayed in its onset and slower in its development than we had anticipated.

After comparatively few successful experiments the excitability of

the nerve suddenly failed, and it is interesting to note that this failure was attended by inability of the organ to respond when a stimulus was applied either to the nerve or to the organ substance. It has been recently pointed out by Garten that if the electrical nerves of *Torpedo* are divided in the living fish, and the fish examined nineteen days afterwards, by which time degeneration of the peripheral portion of the nerve has occurred, no response can be obtained from the organ by any stimulus whether applied to the nerve or directly to the organ

FIG. 1.



The upward curve in the lowest line is a record (No. 3012) of the single shock of 15 mm. of electrical organ evoked by a single excitation of the nerve. The curve is to be read from left to right, the moment of excitation being indicated by the commencement of the larger vibrations on the fine middle line. The rate of movement is shown by the tuning-fork record on the upper line, each complete oscillation of which is 0·002". The electrometer terminals were connected by a resistance of 26·6 ohms, which thus shunted a large proportion of the organ effect.

substance.* These results and the failure referred to in the present instance support the view put forward in our previous paper, that the only excitable structures in the organ are the nerve endings, the organ discs apart from these nerves being inexcitable.†

The Analysis of the Photographic Records.

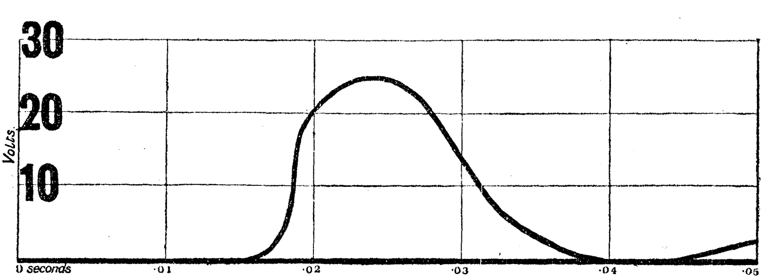
The methods used for obtaining data for the analysis of the records differed somewhat from those employed in our previous experiments upon nerves.

* Garten, 'Centralbl. f. Physiol.,' vol. 13, No. 1, p. 1.
† 'Phil. Trans.,' B, vol. 187 (1896), p. 381.

Since the constants of this particular electrometer had been accurately determined, it might have appeared feasible, after measuring the resistance of the preparation and the resistance of the shunt, to calculate the E.M.F. of the *Malapterurus* shock directly from the photographic record. Such a method would not, however, have been satisfactory, owing to the character of the experimental conditions obtaining in the present research, and it was deemed preferable to obtain the comparison curves given by an E.M.F. nearly comparable with that of the organ response, for the following reasons. The meniscus of the electrometer indicates the E.M.F. acting upon it at any moment, partly by its position above or below zero, and partly by the velocity with which it is moving at that instant, the position being measured in divisions of an arbitrary scale, and the velocity by the subnormal to the curve, expressed in polar co-ordinates. But the ratio between the value of a division on the subnormal and a division on the scale varies with the resistance in circuit, and is consequently affected by the use of a shunt. Obviously, therefore, the simpler method, and the one least open to objection, was to photograph the normal excursion given by an E.M.F. not many times smaller than that of the organ response through a circuit as nearly as possible similar to the actual one, *i.e.*, through an equivalent resistance and through the identical shunt. The organ itself could not be employed for this purpose, because even if it gave no response to such a stimulus, the possible effects of electrolytic polarisation might impart to the record time-relations different from those of a normal excursion.

We therefore carefully measured the resistance of the preparation with the leads in the position employed in obtaining the curves referred to previously (No. 3012 and 3013); we then substituted for it an equivalent non-polarisable, non-inductive resistance, and photographed the excursions given on throwing in a constant E.M.F. of 9 volts through this circuit with a shunt of three-lamps for comparison with the

FIG. 2.



Analysis of No. 3012, showing the E.M.F. of the single shock of 15 mm. of electrical organ, and representing about one-eighth part of the E.M.F. of the shock from the entire fish.

organ shock curve, No. 3012, and a shunt of two-lamps for comparison with the other curve, No. 3013. The curves were then analysed by the method described by one of us.

Both curves gave the same ratio, namely, 15 cm. on the subnormal = 88 scale-divisions on the radius vector. With the three-lamp shunt 120 scale-divisions = 9 volts.

These data, applied to the analysis of the organ shock curves, gave the results detailed in the annexed table. It will be noted that No. 3013, though a much weaker shock, is similar in its time-relations to No. 3012.

Electromotive Force of Shock obtained from 15 mm. of *Malapterurus electricus* Organ.

Time after stimulus, in fractions of a second.	Electromotive force, in volts (No. 3012).	Electromotive force, in volts (No. 3013).
0·0150	0·00	0·00
0·0160	0·44	0·00
0·0170	1·68	0·00
0·0175	3·00	0·00
0·0180	5·20	0·59
0·0185	11·00	
0·0190	17·70	4·25
0·0195	19·40	
0·0200	20·50	8·60
0·0210	22·70	12·80
0·0220	24·00	14·90
0·0230	25·00	15·79
0·0240	25·10	16·15
0·0250	24·90	16·60
0·0260	23·80	16·80
0·0270	22·70	
0·0280	20·20	16·25
0·0290	17·70	
0·0300	14·20	13·85
0·0310	11·70	
0·0320	8·20	11·00
0·0330	6·00	
0·0340	4·90	7·85
0·0350	3·60	
0·0360	2·60	5·15
0·0370	1·75	
0·0380	0·79	3·59
0·0390	0·30	
0·0400	0·00	2·12
0·0440	0·00	
0·0460	0·66	0·00
0·0480	1·92	

In fig. 2 the results of one of the analyses (3012) given in the table are plotted as a curve. This curve may be compared with that of fig. 1, of which it is the interpretation. The ordinates represent the

potential difference between two points, 15 mm. apart, in volts; the abscissæ represent time-intervals after the moment when the nerve was excited.

Comparing these results with those quoted on p. 384 of our previous paper, it will be seen that the initial delay (0·0170 sec. and 0·0180 sec.) is longer than that obtained in our earlier experiments (0·010 sec.), and also that the duration of the organ response is longer (0·0390 sec. instead of 0·021 sec.), although the temperature was nominally the same, viz., 5° C., in both investigations. It must, however, be noted that in the previous research the organ was simply laid upon a glass stage kept at 5° C. by water flowing beneath it, whereas in the present case the preparation was completely enclosed in a large chamber cooled to 5° C.* Undoubtedly the actual temperature of the whole organ strip was higher than 5° C. in our earlier work, and we have ample evidence that in the case of nerve the time-relations of the electrical response are considerably affected by slight changes of temperature at or about 5° C. It should be further noted that the curve now obtained is on a much larger scale than any of those referred to in our previous research, and in consequence the small beginnings of the rise of E.M.F. can be detected at an earlier stage. The curve is that due to the first, or initial, response of a series produced by self-excitation; the commencement of the second member of the rhythmical series caused by such self-excitation is indicated in the plotted curve (fig. 2), but since the object of the experiment was to determine the development of the initial shock, no attention was paid to the other members composing the organ discharge.

The following points brought out by the analysis must be dealt with in more detail:—

(1) There is no trace of any second phase of opposite sign. This characteristic of the organ response is in accord with all previous experiments. It is obviously associated with the circumstance that, since each disc with its nerve endings forms an independent system, no structural basis is furnished for the propagation of the excitatory change from one such system to its neighbours.

(2) The potential difference between the terminals rises more rapidly than it falls (rise, 0·0070 sec.; fall, 0·0160 sec.). Since propagation in the organ does not exist, the rate of development and of decline in the potential difference is the nearest approach yet obtained to the time relations of a localised electrical response in an excitable tissue. It is magnified by the circumstance that such local response occurs almost simultaneously in a whole series of nerve endings. We regard the whole analysis as probably typical of the explosive electrical effect which is evoked in nerve endings when these are at 5° C., and are

* For description of chamber, see Gotch and Burch, 'Journ. of Physiol.,' vol. 24, 1899.

excited by a single stimulus. The elimination of all propagation owing to the structure of the tissue, is a factor of great importance in this connection since such complete elimination is, in our opinion, not experimentally possible in the case of either muscle or nerve. Both the quicker rise and the slower fall may therefore be regarded as expressions of the character of the local change in the nerve endings.

Such a difference between the rate of development and of subsidence of the excitatory explosion was indicated in our earlier experiments, although not referred to in our published paper.* In those experiments we find, on examining carefully twelve different records, the following relation between the duration of the two states, development and subsidence :—

$$\frac{\text{Duration of development}}{\text{Duration of subsidence}} = \frac{265}{326}, \text{ or } \frac{81}{100}.$$

In the present instance, possibly owing to the more effectual cooling, the more prolonged character of the subsidence is very conspicuous.

Thus in the two analysed instances, here referred to, we find

$$\frac{\text{Duration of development}}{\text{Duration of subsidence}} = \frac{7}{16}, \text{ or } \frac{44}{100}, \text{ and } \frac{8}{17}, \text{ or } \frac{47}{100}.$$

One other point of interest in connection with the development of the E.M.F. is the comparatively gradual character of its actual commencement. The analysis shows that for 0·002 second after a potential difference can be detected, its value is relatively small.

It might be objected that the gradual development and still more gradual subsidence of the E.M.F. may have some purely physical explanation apart from the physiological change in the nerve endings, such, for instance, as polarization capacity due to the special structure of the tissue. That this is not the case is clearly proved by experiments in which a strong induction shock traversed the organ, which failed to excite it but was itself recorded on the plate. We have several examples of induction shocks of different intensities, of condenser discharges, and of excursions due to transient currents through the same circuit. In none of these is there any resemblance to the peculiar form of the curve given by the organ response. We are therefore in a position to say that the time relations of the organ shock do not resemble those of either induction currents, condenser discharges, or currents of short duration from a source of constant E.M.F.

(3) The duration of the period between the excitation of the nerve and the commencement of the organ response (0·017 sec.) represents the transmission time of the excitatory state along 40 mm. of nerve fibre when cooled to 5° C., this being the distance between the seat of

* 'Phil. Trans.,' B, vol. 187 (1896), p. 347.

excitation and the organ strip. It is probable that the greater part of this time is occupied by the slow transmission of the excitatory state along the finest sub-divisions of the nerve within the organ near the ultimate nerve endings, all of which were at 5° C.

(4) The most interesting point in connection with the whole experiment is the maximum E.M.F. attained by the response given by the small portion of organ (15 mm.) investigated; this amounted to 25·10 volts in the most favourable instance.

The contacts were 15 mm. apart, and we convinced ourselves that localised excitatory changes in the piece of tissue situated between these contacts were responsible for the development of the electrometer movements when our apparatus was arranged as indicated in the opening description. This piece of tissue was subsequently removed and appropriately fixed for microscopic examination. Sections were then cut so as to display all the discs lying between the points of the electrode contacts. The recent work of Ballowitz has shown that the nerves do not reach the expanded discs, but end in their caudal stalks. The discs themselves are contained in the lozenge-shaped compartments constituting the columns. These are so situated that one columnar row of compartments is dove-tailed into those of all its neighbours. The result is that the number of discs and stalks in longitudinal series is twice as many as the number of lozenge-shaped compartments constituting any given column. Enumeration of the successive compartments in a number of different columns throughout the portion of organ between the contacts (15 mm. long) gave the following figures: 260, 265, 262, &c. It was therefore assumed that the electromotive difference of 25·10 volts was probably distributed uniformly over a series of at least 530 discs; the maximum E.M.F. of the change in any one disc, with its nerve endings, would thus be not more than 0·048 volt. It is of intesest to note that in the sciatic nerve of the frog we have obtained an excitatory effect amounting to 0·033 volt.

(5) The whole organ of the fish measured 12 to 15 cm. The extreme ends are thinned down, but it may be certainly inferred that 12 cm. of this organ would be at least as functionally active as the portion we investigated. This would give a development of 200 volts for the whole series of organ discs, and even this high value cannot be regarded as a maximum for the living fish, since it was evident to us that the organ preparation we employed had its functional activity lowered both by the low temperature and by the operations involved in its dissection. It is worth noting that during the first stages of the dissection carried out on the entire fish cooled in ice-cold water to anæsthesia, the division of a nerve branch with metal scissors whilst the organ was grasped by metal forceps, caused a strong shock to pass through the arms of the operator (F. G.), which was felt up to the elbows.

It must be self-evident to anyone who makes the experiment that the phenomena resulting from the passage of the organ shock through the human body are such as cannot be produced by interrupted battery currents unless the potential is high. It is a matter of common knowledge that the shock from a healthy fish will pass through a chain of several people holding hands, and will be felt by each, not only in the arms, but in the muscles of the chest and shoulders. No battery current of 30 or 40 volts through such a circuit will do this, however interrupted, unless the circuit has considerable self-induction, in which case the E.M.F. of the battery does not represent the E.M.F. of the shock, which may greatly exceed it.

It is, therefore, surprising that D'Arsonval's investigations led him to give 17 volts, and that Schönlein gives 31 volts as the maximum E.M.F. of a *Torpedo* shock. Such low numbers indicate, we think, that the methods used by these observers were not applicable to the measurement of the maximum E.M.F. of the shock of an electrical organ.* This opinion was stated definitely in our paper, and we here repeat the statement because the photographs now published show plainly that the development of the E.M.F. of an organ shock is, at low temperatures, comparatively slow, much less rapid in fact than that of a battery current thrown in by breaking a short circuit. So far, therefore, as suddenness of change is concerned, the electrical organ is, under these conditions, at a disadvantage as compared with a battery current; yet it can produce muscular contractions such as can only be caused by interrupted currents of high potential. We are, therefore, constrained to believe that the maximum E.M.F., even in *Torpedo*, will be found to be nearer 200 than 30 volts. At any rate the analysis of the foregoing curves indicates that this maximum, namely, 200 volts, is attained by the organ shock of *Malapterurus electricus*.

The Electrical Resistance of the Electrical Organ.

Owing to the failure of the organ to respond to further excitation, it was impossible to carry out the other experiments which we had contemplated. We therefore decided to make such measurements of the electrical resistance of the tissue as could be effected with the apparatus at hand. In the absence of a Kohlrausch bridge we employed a resistance-box of the Post Office type, and used the capillary electrometer as an indicator. With this instrument it is advantageous to have the bridge arms of the highest available resistance—in this case 1000 ohms : 100 ohms—as the current is thereby reduced, while the excursions are in no way lessened. For a similar reason a shunt is not employed, but the current is derived from a rheocord

* D'Arsonval, 'Comptes Rendus,' vol. 121, p. 145, 1895; Schönlein, 'Zeitsch. f. Biol.,' vol. 31, N. F., 13.

instead of a battery, the potential being kept low until a balance is nearly obtained. Square blocks of the organ of various dimensions were placed on a glass slip, and broad cables of lamp-wick pasted over with kaolin and salt solution used to connect them with the ordinary non-polarisable electrodes. After each measurement the cables were joined together without the interposition of the organ strip, in order to ascertain the resistance due to the leads. It was found that the variation in resistance of the leads between one experiment and another was relatively inconsiderable, the greater part of the electrode resistance being evidently due to the unexposed portions of the non-polarisable electrodes, *i.e.*, the tubes containing saturated zinc sulphate. The direction of the current was reversed from time to time, but such reversal was not found to exercise any marked influence upon the results.

The differences in the extensibility and elasticity of the superficial and deep boundary walls of the organ offered a difficulty, since it was found to be almost impossible to cut the organ into blocks which should be of the same superficial area on these two aspects. Care was, however, taken that in every case the dimension in the direction of the length of the columns (*i.e.*, head end to tail end) should be, if anything, less than that in the direction across the length of the columns (*i.e.*, transverse). These two dimensions will for brevity be termed, the first, longitudinal, the second, transverse, the words indicating their relationship to the organ column.

It must be remembered that the line of flow of a current directed longitudinally is transverse to all the flattened discs which are placed athwart the columns—whilst that of a current directed transversely to the column is parallel with these thin discs. On *primâ facie* grounds we should expect that the resistance in the former case would be far larger than that in the second if, as seemed certain, the thin disc subtance has an electrical resistance which is far above that offered by the remaining space of the compartment and the albuminous substance with which this is filled.

This expectation was fully realised by the experimental results, of which the following table gives examples :—

Resistance of Block of Electrical Organ.

Dimensions.			Resistance.	
Longitudinal.	Transverse.	Thickness.	To longitudinal current flow.	To transverse current flow.
mm.	mm.	mm.	ohms.	ohms.
10	10	3	2700	600
15	15	3	2800	1300
12	13	3	3100	1300

The resistance to the flow of a current in the longitudinal direction (*i.e.*, directed across the disc surfaces) is thus from two to three times as great as that offered by the organ to the flow of a current in the transverse direction (*i.e.*, directed parallel to the disc surfaces). The discs themselves thus offer, when their physiological condition is unimpaired, a high resistance as compared with the adjoining compartmental contents, and this result is corroborated by experiments made after the conditions had been modified either physically or physiologically. The physical modification consisted in taking blocks, the longitudinal dimensions of which varied. Thus a block 10 mm. in the transverse dimensions and 3 mm. in thickness, was cut so as to be 90 mm. in the longitudinal dimension. Its resistance to the flow of a longitudinal current amounted to 27,600 ohms. On reducing its length to 40 mm. the resistance was 13,000; on reducing it to 20 mm. it was 5700, and on reduction to 10 mm. it was 2700 ohms. The heavy longitudinal resistance is seen to increase in proportion to the length of the columns, and the results thus indicate that our method was a fairly accurate one.

The physiological modifications were produced both by destroying the living condition of the fresh tissue by a suitable rise of temperature and by keeping the tissue in physiological saline for a number of hours, so that the living condition should be more or less replaced by one due to commencing natural death.

In the case of destruction through heat, the striking discrepancy between the large resistance offered to longitudinal currents, and the lower one offered to transverse ones, always disappeared completely. The resistance was now found to be the same whatever the direction of the current flow.

In the case of kept preparations, the disparity between the two resistances became so much the less marked as the preparation lost its living characteristics; thus a preparation which had been kept 24 hours in saline still showed 1500 ohms longitudinal resistance, as compared with 500 ohms transverse; whilst a second strip, kept for 48 hours, showed only 1000 ohms longitudinal, as compared with 800 ohms transverse.

There is thus little doubt that the greater resistance offered by the columns of the fresh organ to longitudinal flow of currents is due to the circumstance that these are directed through the protoplasmic substance of the thin plates or discs, which, lying directly athwart the columns, are all so interposed in the line of flow as to give a maximum of protoplasm to be traversed by such a flow. On the other hand the small resistance offered to transversely directed currents is an expression of the fact that the flattened protoplasmic discs now form but an insignificant portion of the conducting medium, which is chiefly composed of the compartment spaces. The discs must therefore have

a relatively high resistance as compared with that of the albuminous fluid filling the remainder of the space. It has been sometimes suggested that alterations of resistance may play an important part in the phenomena of organ activity. The experiments just given appear to indicate that the discs have a resistance which is of a different order to that of the physiological saline in the surrounding media; but even in the case of these protoplasmic structures the results scarcely warrant the belief that there is anything exceptional in their higher resistance since it only places them in the same category with such other excitable tissues as muscle and nerve, which have been shown to offer a greater electrical resistance in the transverse than in the longitudinal direction.

On the Formation of the Pelvic Plexus, with especial Reference to the Nervus Collector, in the Genus *Mustelus*." By R. C. PUNNETT, B.A., Scholar of Gonville and Caius College, Cambridge. Communicated by HANS GADOW, F.R.S. Received June 30,—Read November 16, 1899.

(Abstract.)

The main object of this investigation was to ascertain whether at any period in the development of the animal selected, the number of branches composing the *nervus collector* was greater than that found in the adult. As a logical consequence of Gegenbaur's theory we should expect such to be the case, and the ontogenetic history of the *nervus collector* recorded in this paper, its maximum development in young embryos, and its subsequent gradual decrease through the later stages of embryonic existence leading to its condition in the adult, must, if there is any truth in the recapitulation theory, all point to its primitive character.

The history of the posterior collector, the very existence of which has not hitherto been described, throws important light upon the theory mentioned above. Here we have a collector formed in the embryo, from which in later stages the component nerves separate and run singly into the fin. Such a fact points very strongly to the collector condition being more primitive than that condition in which the nerves reach it without previously effecting any junction with one another.

It is further shown that the formation of this collector is due to migration of the whole fin rostrally, and not merely to a contraction of the fin area, and in support of this the following evidence is brought forward. The two species, *M. lævis* and *M. vulgaris*, differ from one another chiefly in the more rostral position of the pelvic girdle in the former. That it is highly improbable such a condition should be due