

CIRCULATION IN A GIANT EARTHWORM, *GLOSSOSCOLEX GIGANTEUS*

I. CONTRACTILE PROCESSES AND PRESSURE GRADIENTS IN THE LARGE BLOOD VESSELS*

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The annelid worms stand out among most other invertebrate forms by having a closed vascular system. Their blood usually contains haemoglobin in simple solution as a respiratory pigment. Some of the earthworms as a subdivision of this phylum may attain considerable size weighing more than 500-600 g., and may be as long as 120 cm. with a maximum diameter of 2-3 cm. It is surprising to find that the earthworm *Glossoscolex giganteus* of such great size has no special organs of respiration, the skin being the only surface available for gas exchange. Such a structural arrangement may depend upon specialized adaptations in the pattern of blood flow or in the respiratory characteristics of the blood, or both.

The present investigation aims at describing some parameters of circulatory transport in the larger vessels of the giant earthworm, *G. giganteus*.

MATERIAL

Most of the experiments to be described were done in Sao Paulo, Brazil. The earthworm, *G. giganteus* is readily available in the tropical and subtropical regions of Brazil. The animals were collected by digging the soil, often to the considerable depth of 100 cm. or more. From the various collecting sites the animals were transported in moist soil to the laboratories in Sao Paulo. A new supply of animals was brought to the laboratory every week on the week-end. When kept in moist fairly cool soil (15-20° C.) the animals could be retained in good condition for 2-3 weeks.

The radiological studies were done in Oslo, Norway, on animals shipped by air from Sao Paulo, Brazil. Five out of eight animals survived the long journey in excellent condition.

The species *G. giganteus* is one of the largest of all earthworms. Specimens have been reported to reach the truly amazing length of 1.26 m. (Stephenson, 1930). Members of the genus *Glossoscolex* are distributed in tropical South America, along the eastern part from the Brazilian states Minas Gerais in the north to Rio Grande do Sul in the south.

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The vascular system of oligochaetes and, earthworms in particular, has been thoroughly analysed from an anatomical viewpoint. The monograph of Stephenson is an authoritative and valuable source of detailed information. In the present context it will suffice to recall some of the most essential anatomical features of the vascular system of an earthworm.

All closed vascular systems are arranged in collecting and distributing vessels usually with a central focus or meeting site in a propulsive blood-pumping mechanism. Apart from the central pumping mechanism auxiliary mechanisms for blood propulsion can be spaced throughout the vascular channels. In the earthworms the largest vessel, the dorsal vessel, constitutes the most important collecting vessel. This vessel is the most conspicuous in the animal. It is found dorsal to the alimentary canal and traverses the entire length of the body. It is closely adherent to the gut except in the anterior region of the lateral hearts. It ends anteriorly on the pharynx. As the main collecting vessel it receives blood from the dorso-intestinal vessels and the dorso-subneural commissures. The dorsal vessel has an inherent rhythmic peristalsis in postero-anterior direction driving blood forwards. In front of segment 12 the dorsal vessel ceases to be a collecting vessel. The vessel now gives rise to the five pairs of large commissures to the ventral vessel. These commissures contain the lateral hearts, often called pseudohearts. These hearts provide the pumping power needed to set up the distributing flow of blood.

The ventral vessel thus constitutes the main distributing channel. Behind the hearts flow takes place in the posterior direction. It is conveyed to the parietes and nephridia by the ventro-parietals, and to the intestine by the ventro-intestinals (Stephenson, 1930). Anterior to the hearts the distributing flow in the ventral vessels takes place in forward direction. In the subneural and lateral neural vessels the flow is reported to have a posterior course (Stephenson, 1930). The ventral vessel is recognized as having no peristaltic activity comparable to that of the dorsal vessel.

METHODS

Anaesthesia

It proved very difficult to find a suitable anaesthetic for use on the giant earthworms. The most satisfactory consisted of a 5% solution of propylene phenoxytol in water. A gentle bathing in this solution for 3-5 min. provided in general enough muscle relaxation to enable the intravascular catheterizations to be performed. At times the animals went through an excitatory stage with vigorous motor activity. In such conditions the earthworms are very susceptible to autotomy. Important advantages of the anaesthetic were the high safety level and the quick recovery time. Forty to sixty minutes after induction of anaesthesia the animals were in general in normal active condition.

Operative procedures

Upon induction of suitable muscle relaxation an earthworm was transferred from the solution of propylene-phenoxytol to the operating table and placed on moist paper. When cannulations were made for simultaneous recordings of pressures in the dorsal and ventral vessels an incision was first made dorsally in segment 8. A 15 mm. incision was made extending transversely from about 10 mm. dorsal to the setae on one

side ending in the same point at the contra-lateral side. The incision followed the septum closely on its posterior side. By careful dissection with a blunt instrument the dorsal vessel was freed from adjoining tissue anterior to its bifurcation into the two lateral hearts of the segment. Two ligatures were passed under the vessel. The catheters used were of standardized length (30 cm.) made of 20- or 50-gauge polyethylene tubing and filled with earthworm Ringer. The catheter was passed from 10 to 15 mm. in the posterior direction (upstream). The method of cannulation will of necessity obstruct flow anterior to the point of cannulation. This will at the most involve impairment of the most anterior set of lateral hearts. These are by far the smallest and their contribution to the total circulation is relatively minor. After the catheter had been tied in place a supporting suture was applied to maintain the catheter in an antero-posterior direction, to avoid kinking and possible extravasation as a result of the catheter tip cutting through the vascular wall. The supporting suture was in general applied between the catheter and a holding point in the adjoining forward septum between segments 8 and 9. The catheter was guided out through the body-wall and the primary incision was closed with interrupted sutures.

A similar technique was used when cannulating the ventral vessel. This vessel was cannulated at a number of levels as far back as segments 40-45 and as far forward as segments 18-20. In this cannulation the catheter was passed in an anterior direction (upstream). The pressures obtained turned out to be independent of the level of cannulation. This indicates that commissural circulation is adequate to compensate for the obstruction presented by the catheter. To substantiate this, cannulation was also made of the ventral vessel anterior to the most forward pair of lateral hearts (segments 6-8). In this case the catheter was, of course, passed posteriorly. The general level of pressure, and also the pulse pressures, were of the same order, giving reassurance that the method of cannulation does not unduly disturb the normal haemodynamics.

The catheters provided access for simultaneous measurements of pressure as well as for sampling of blood or injections of drugs. Catheters were successfully maintained in place for periods of up to 6 days.

In preparation for the angiographic studies the catheterization was made in the dorsal vessel with the catheter pointing in anterior direction (downstream). The level of catheterization was usually in segments 50-70.

Pressure recordings

The pressure-recording equipment consisted of Statham pressure transducers P23 BB of the most sensitive type. The transducers were connected to an Offner dynograph amplifier and recording system. The recordings were rectilinear and traced by a stylus heat system. In general two pressures were recorded simultaneously; however, in some instances the intracoelomic pressure changes were monitored together with dorsal and ventral vessel pressures. The recordings were made with the animals fully recovered from anaesthesia and placed on moist paper or in a simulated normal situation buried in moist soil. Pressure recordings were obtained from animals in resting and active condition as well as in conjunction with drug injections. Experiments were also carried out on anaesthetized animals and on fragments of animals subsequent to autotomization.

Angiographic studies

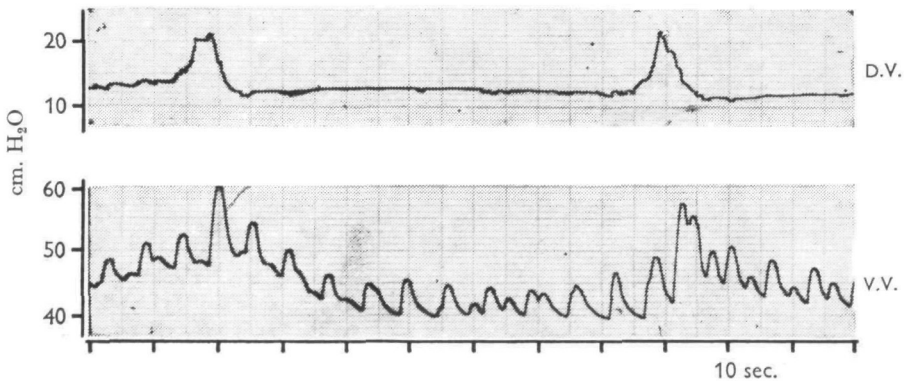
The radiological part of the investigation was carried out in Oslo, Norway. The equipment utilized consisted of an Elema Schönander film changer. This equipment operates with 20 × 20 cm. film and offers the advantage of a high degree of resolution. The rate of exposure could be varied up to six frames per second. Exposures were made at 50 kV. and 200 mA. Exposure time was 0.02 sec., film focus distance 90 cm. with a focus size of 1.2 × 1.2 mm.

The contrast medium used was isopaque 'NYCO' 60%. The medium was injected through a catheter in the dorsal vessel (see earlier description). The position of the catheter was checked by fluoroscopic control. Exposures were taken in dorso-ventral projection as well as in lateral projection.

RESULTS

Pressure measurements

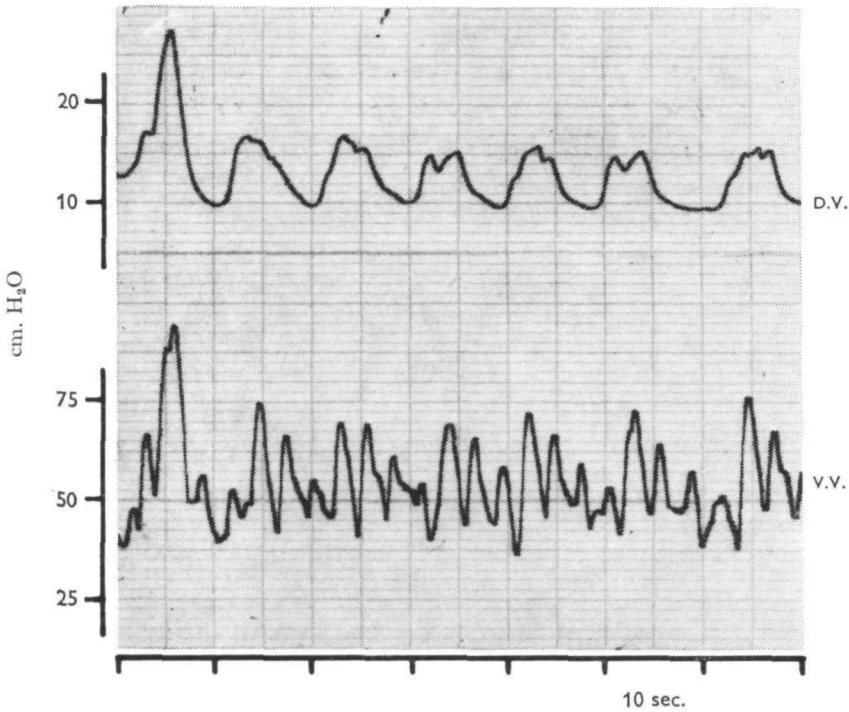
The pressure measurements were designed to elucidate the pressure gradient from the dorsal vessel through the commissural hearts to the ventral vessel. It was also considered important to assess the frequencies of contraction in the various segments and how these were interrelated.



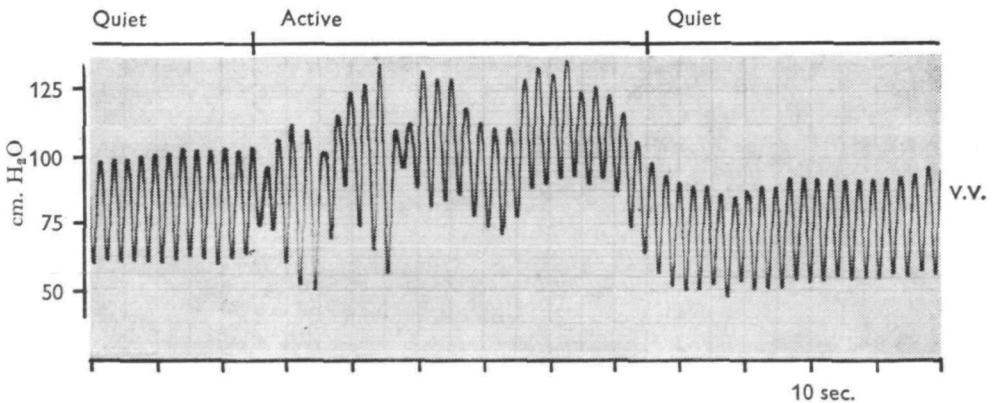
Text-fig. 1. Simultaneous pressure recordings from the dorsal vessel (D.V.) and the ventral vessel (V.V.) of an unanaesthetized resting earthworm *Glossoscolex giganteus*. Temperature 18–20° C.

In fully recovered animals lying quietly there was distinct difference in frequency between the peristaltic contractions in the dorsal vessel and the contraction of the lateral hearts. The peristaltic contractions were always the slowest but also the most variable. Text-figs. 1 and 2 show simultaneous pressure recordings from the dorsal and ventral vessels in two different animals. The difference in frequency of the two contractile processes is readily apparent. In Text-fig. 2, however, the frequency of peristalsis in the dorsal vessel is considerably higher than in the animal providing record 1. The average resting frequencies for twenty animals were 8 and 20 per minute for the dorsal and ventral vessel, respectively. A fundamental problem concerning frequency relations is to what extent the five pairs of hearts beat in synchrony or randomly. Most recordings indicate that a synchronous contraction is the more

common although unco-ordinated—and hence less efficient—contractions often were detected, particularly during and after vigorous movements. Text-fig. 3 shows a tracing from the ventral vessel indicating a complete synchrony in contraction of the lateral hearts, both during rest and exercise (there were three pairs of hearts with free flow in this animal). The surprisingly high pressures, exceeding 125 cm. H₂O during the most active period, are to be noted; also that there is no apparent change in

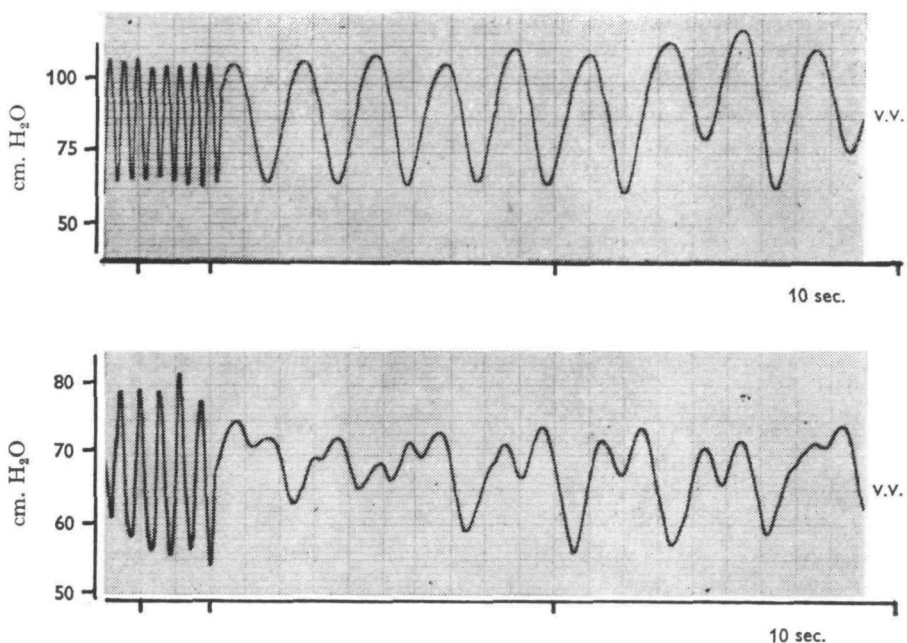


Text-fig. 2. Simultaneous pressure recordings from the dorsal and ventral vessel. Note the marked difference in the frequency of the two tracings. Temperature 18–20° C.

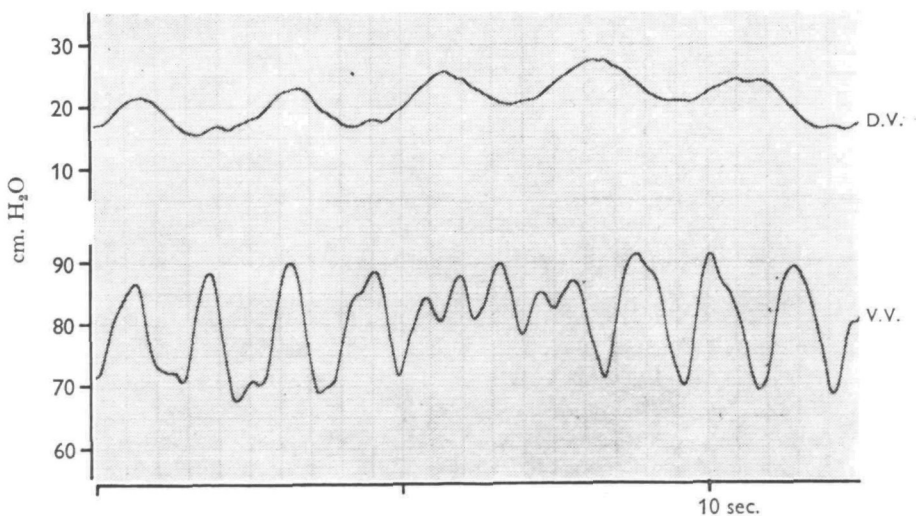


Text-fig. 3. Ventral vessel pressure tracing from healthy, active earthworm. All the lateral hearts beat in perfect synchrony. Temperature 18–20° C.

frequency during or after the period of activity. Text-fig. 4, from another animal, shows examples of synchronous and asynchronous contraction of the lateral hearts. The asynchronous contraction in the bottom tracing shows lower and more irregular pressures. Text-fig. 5 demonstrates a transient period of asynchronous contraction.



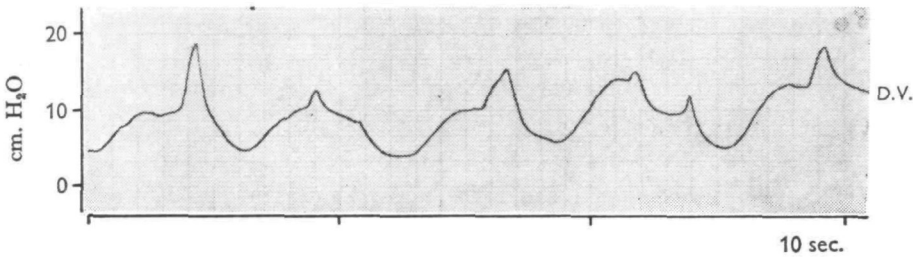
Text-fig. 4. Two pressure tracings from the ventral vessel showing synchronous (top tracing) and asynchronous contractions of the lateral hearts. Temperature 18–20° C.



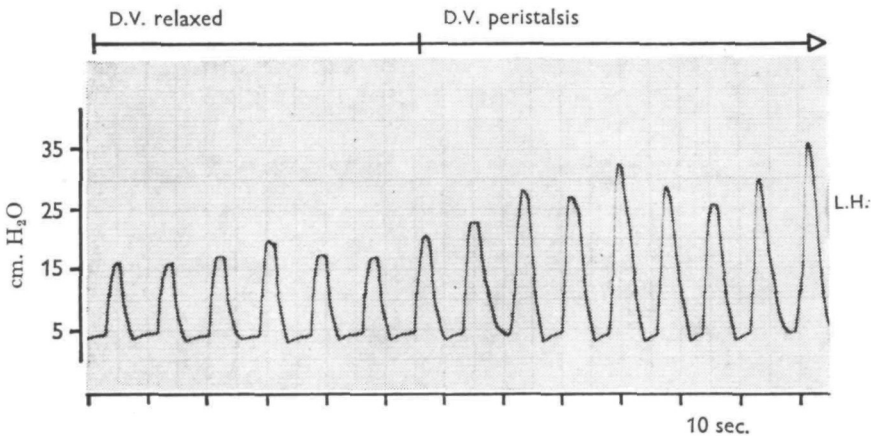
Text-fig. 5. Simultaneous pressure tracings from the dorsal and ventral vessels. The ventral vessel tracing reflects a transient period of asynchronous contraction of the lateral hearts. Temperature 18–20° C.

This occurred during a slight motor movement of the animal which was associated with an increased pressure in the dorsal vessel.

Another demonstrable phenomenon from most of the pressure tracings is the great competency of the valves located between the dorsal vessel and the entrance to the lateral hearts. In almost all tracings from the dorsal vessel one can notice secondary pressure pulses caused by the back pressure against the valves from the contracting



Text-fig. 6. Pressure tracing from the dorsal vessel. Note the superposed shorter lasting pulses reflecting the back pressure against the valves between the dorsal vessel and the lateral hearts. Temperature 18–20° C.

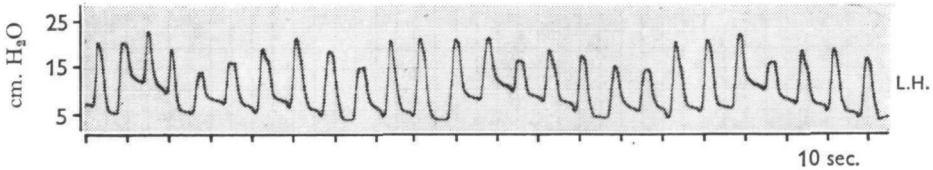


Text-fig. 7. Pressure recording from inside the lumen of one lateral heart. The last half of the record shows the response to a dorsal vessel peristalsis. Temperature 18–20° C.

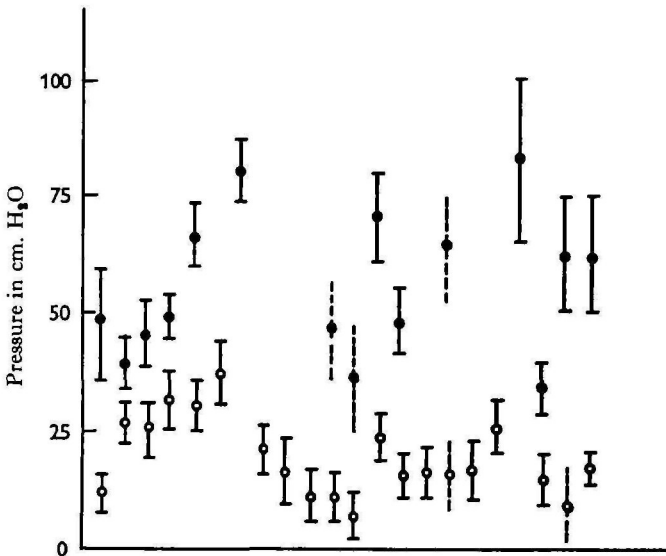
hearts (Text-figs. 1–4). In Text-fig. 6 it seems significant that these superposed pressure peaks always occur when the peristaltic pressure wave has reached peak pressure. This may indicate that the filling of the lateral hearts by the peristalsis in the dorsal vessel may be a participating factor in the timing of the heart contractions.

That the filling of the hearts, effected by dorsal vessel peristalsis, is of paramount importance for their force of contraction and general performance was clearly demonstrated from the pressure tracings. In Text-fig. 1 A and B there is a marked augmentation in the ventral vessel pressure concurrent with each peristaltic wave. Between the peristaltic contractions the pressures created in the ventral vessel by the contracting hearts may drop to $\frac{1}{6}$ – $\frac{1}{8}$ of the values during the most active phase of the peristaltic contractions. In Text-fig. 1 B the maximum pulse pressure in the ventral vessel

coincides with peak pressure in the dorsal vessel. The tracing shows a pulse pressure of more than 15 cm. H_2O dropping to less than 5 cm. H_2O during the resting phase in the dorsal vessel. In one animal it was possible to obtain pressures from inside the lumen of one lateral heart; text-fig. 7 demonstrates the intracardiac pressure in this animal. At the start of a peristaltic contraction in the dorsal vessel the contractile force of the heart swiftly increases. Text-fig. 8 shows the same phenomenon and also



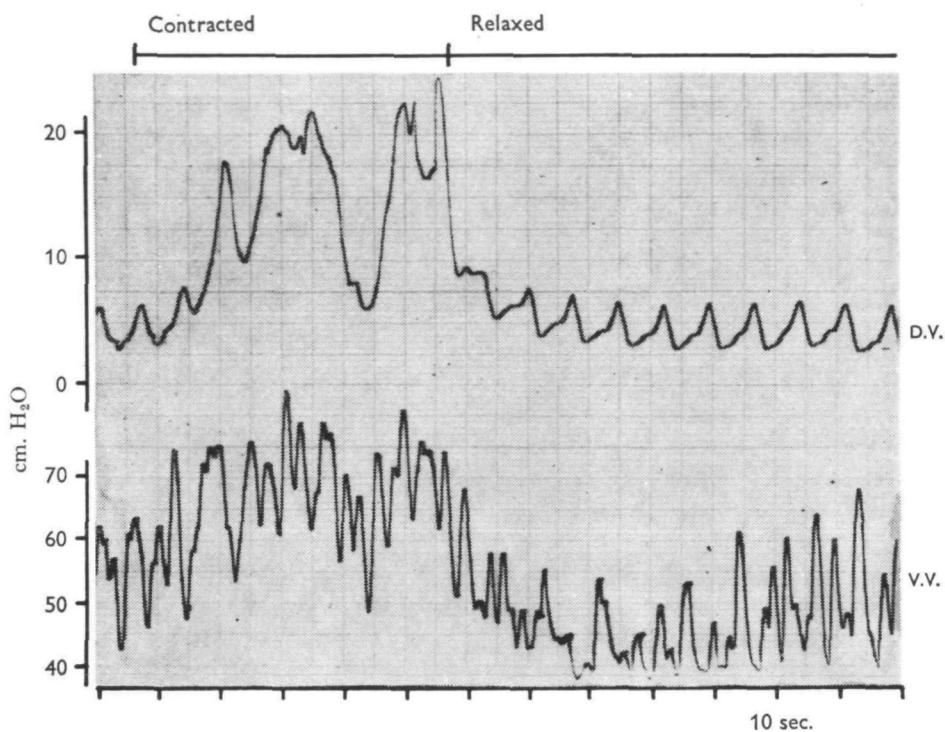
Text-fig. 8. Pressure recording from one lateral heart. The slower phasic shifts in diastolic pressure are caused by the dorsal vessel peristalsis. Temperature 18–20° C.



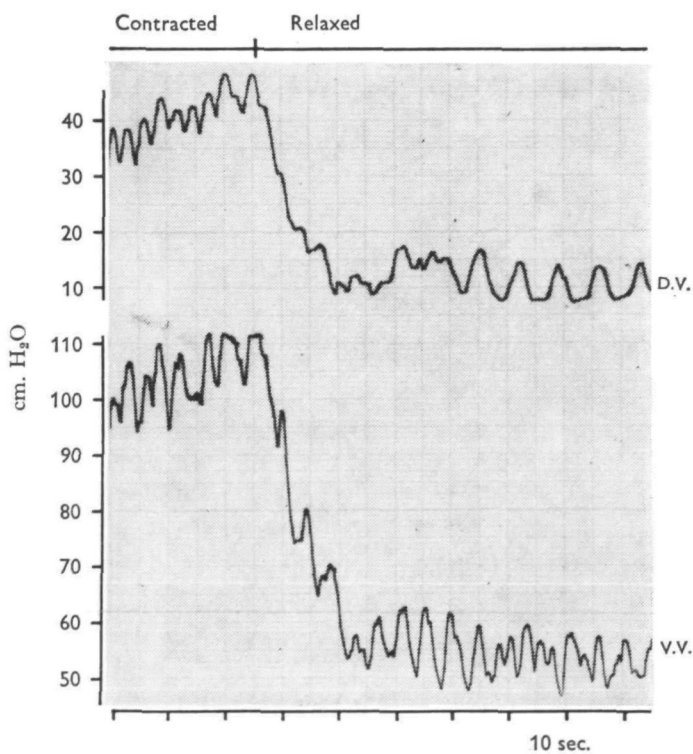
Text-fig. 9. Intravascular pressures from the dorsal and ventral vessels of the giant earthworm in a composite diagram. The dorsal vessel is represented with open circles. The filled and open circles represent the average values while the bars indicate the systolic and diastolic values. The dotted lines are filled in when only average values were obtained. Temperature 18–20° C.

that the filling of the hearts during the peristaltic contraction is so large that the intracardiac diastolic pressures show a transient increase. There was no significant change in the rate of heart contraction during the increased filling.

The general levels of pressure in the dorsal vessel and ventral vessel during resting conditions appear from Fig. 9. In spite of the large variability in absolute pressure values one can appreciate a relatively uniform pressure gradient from the dorsal to the ventral vessel. The average systolic pressure in the dorsal vessel was 24 cm. H_2O (average of 16 animals), while the average diastolic pressure was 14 cm. H_2O . In a few animals the diastolic pressures are seen to be below 5 cm. H_2O while similarly a few animals have systolic values between 35 and 40 cm. H_2O . In the ventral vessel the



A

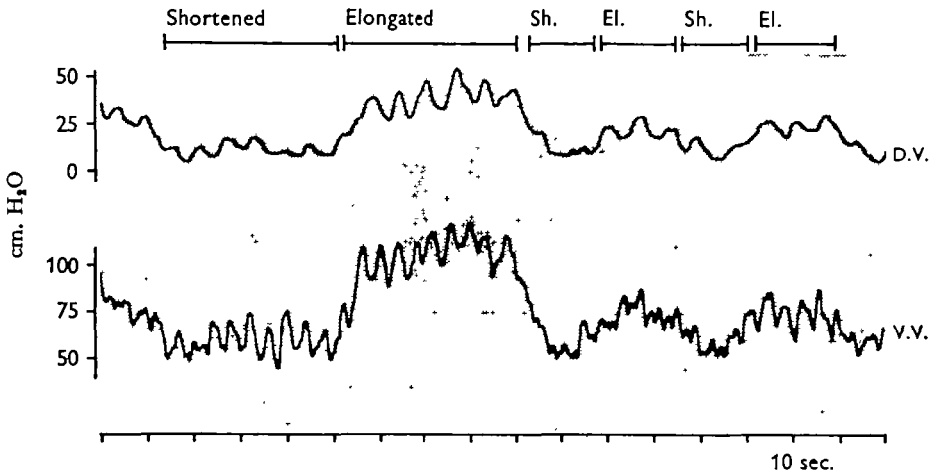


B

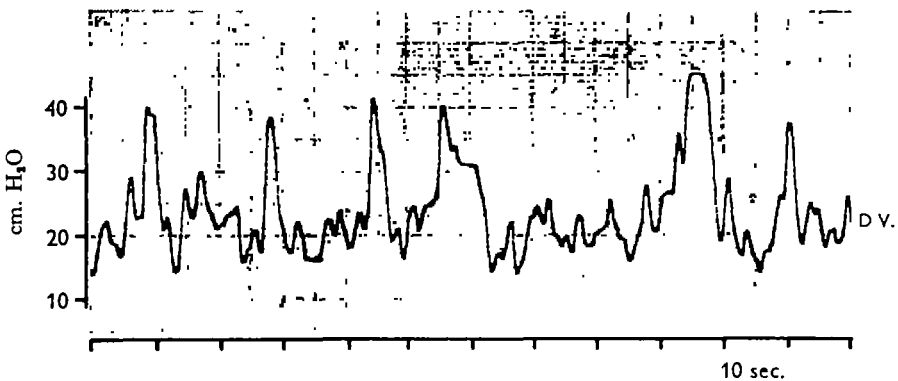
Text-fig. 10 A, B. Simultaneous pressure tracings from the dorsal and ventral vessel in two different earthworms during periods of transient activity. Temperature 18–20° C.

pressures have increased conspicuously with average values of 65 cm. H₂O systolic and 47 diastolic for 13 animals. The average pulse pressures in the two vessels were 10 cm. H₂O and 18 cm. H₂O in the dorsal and ventral vessels respectively.

Intravascular pressures were also recorded from the giant earthworms when they were actively moving around on moist paper or clothing in air, or burrowing in soil.



Text-fig. 11. Dorsal and ventral vessel pressure recordings during motor movement of an earthworm. The movement is brought about by successive shortenings and elongations of the body-wall. Temperature 18–20° C.



Text-fig. 12. Dorsal vessel pressure recording from an active earthworm buried in 20–30 cm. of hard-packed moist soil. Temperature 18–20° C.

The general body-wall of the earthworm is equipped with powerful muscles. During active movement the state of contraction of the body musculature must obviously exert a decisive effect on the coelomic and intravascular pressures. The pressure tracings during active movement will hence have a more irregular appearance and the rhythmic activity of the inherent cardiovascular contractions may be somewhat obscured. It is, however, immediately apparent that the general level of intravascular pressures increased significantly when the body wall contracted. Text-fig. 10A and B demonstrate a transient period of body-wall contraction. The intravascular pressures

are seen to be almost doubled. The peristaltic contractions appear obscured, but are quickly re-established to perfect rhythmicity when the body-wall relaxes again.

The motor movement of an earthworm is brought about by peristaltic contractions of the body-wall musculature. These contractions can include shorter or longer sections of the animal and they move along the animal axis in a direction depending on whether the animal moves forward or backward. In effect these contractions bring about alternating shortenings and elongations of the animal. During a shortening the body-wall will exert less pressure on underlying soft structures whereas an elongation will have the opposite effect. Text-fig. 11 demonstrates how these alternating shortenings and elongations are reflected in the intravascular pressures. They are seen to exert a substantial effect on the levels of pressure. The seemingly erratic pressure tracing in Text-fig. 12 was obtained from the dorsal vessel of a very vigorous and healthy earthworm covered by 20–30 cm. of relatively hard-packed moist soil and presumably forming a burrow.

Radiological analysis

Pl. 1 shows a series of roentgen frames demonstrating successive stages of the passage of the contrast medium from the dorsal to the ventral vessel. The exposures were taken in slightly oblique lateral projection. The segmentation of the animals is clearly discernible in the dorsal vessel which has the appearance of a string of pearls. Frame (1) shows a maximal filling of the dorsal vessel. The lateral hearts are also filled, but clearly not to the same degree. The two most posterior pairs of hearts always showed a better filling. In frame (1) the ventral vessel is distinctly delineated from previous heart contractions. The vessel can also be followed in the anterior direction extending rostral to the large oesophageal gizzard. In frame (2) one can see a peristaltic contraction in the dorsal vessel travelling forward from the far right of the frame. The filling of the hearts becomes more uniform. The ventral vessel meanwhile gets less conspicuous. In frame (3) the dorsal vessel peristalsis has propagated clearly to the heart region. It seems noteworthy that the peristaltic contraction has reduced the lumen of the dorsal vessel practically to nothing. Although still distended, at least one or more of the lateral hearts have now contracted since renewed filling of the ventral vessel can be observed. It should be emphasized that the lateral hearts did not display a synchronous contraction in any of the radiological examinations. This fact made it difficult to evaluate the possible residual volumes of the hearts. Within these limitations the residual or end systolic volumes of the hearts seemed far larger than the same for the dorsal vessel subsequent to peristalsis. In frame (4) the ventral vessel seems maximally dilated. Its largest cross-section is considerably less than the maximum cross-section of the dorsal vessel.

Pl. 2 depicts a length of the dorsal vessel during propagation of a peristaltic contraction. Loops of lateral segmental vessels connected to the dorsal vessel are clearly discernible. Frame (1) shows the dorsal vessel during maximal filling. At least twenty-five dorsal vessel segments are distended with fluid. In frame (2) a peristaltic contraction can be seen beginning at the lower end of the frame. In frame (3) the peristalsis has travelled to the upper end of the frame. An approximate count indicates that the peristalsis travels at a speed of about 12 segments per second. Frame (3) allows a count of how many segments are contracted at the same time. Between 20 and

25 segments show a marked simultaneous contraction of the dorsal vessel. Approximately equal lengths of vessel may therefore alternate in contraction and relaxation.

Comparing frames (2) and (3) there is a conspicuous disappearance of the numerous vascular loops connecting to the dorsal vessel. One possible explanation may be that these smaller vessels by peristaltic contraction have emptied into the large dorsal vessel. All of the frames seem to show a single pair of lateral segmental vessels. Perhaps these are filling from the dorsal vessel and peristalsis may have continued into these smaller vessels and emptied them in the opposite direction. The problem of local circulation is a difficult one and this matter will be discussed later. The earlier anatomical finding is that both the dorso-intestinals and dorso-parietals are afferent vessels to the dorsal vessel (Johnston, 1903).

The time lapse between individual peristaltic contractions evaluated by the radiological examinations was in general agreement with the time sequence obtainable from the pressure measurements. Again one should emphasize the marked degree of vessel constriction during peristalsis.

DISCUSSION

The many papers on circulation in earthworms are all of limited consequence to the understanding of the physiology of circulation, owing to inadequate methods of investigation. Without exception visual observations of the larger blood vessels and hearts have formed the basis for the acquired information. The general course of circulation in the larger vessels of many transparent forms has however been adequately evaluated. The works of Johnston (1903) and Johnston & Johnson (1902) on *Lumbricus* still provide the framework for the teaching adopted on this subject. Later works of Bahl (1921) and Aoki (1930) studying *Pheretima*, and Haffner (1927) working on *Lumbriculus* confirm the general ideas proposed by Johnston (1903). Other workers have specifically studied the peristaltic contractions of the dorsal vessel of earthworms. Biedermann (1904) and Stübel (1909) have offered substantial but purely descriptive contributions to that field.

The circulatory system of the oligochaetes can be conveniently analysed by division into collecting and distributing vessels connected by a main propulsive element, the hearts. In any closed vascular system the mechanisms for collecting and returning blood to the hearts are the main determining factors for the output from the heart. It seems appropriate to start by analysing these mechanisms in the giant earthworm *Glossoscolex giganteus*.

The rhythmic peristaltic activity inherent in the dorsal vessel originates in general in the posterior end of the animal. The effectiveness of the peristalsis of the dorsal vessel in propelling blood seems high. The intravascular pressures developed by the peristaltic contractions reached 25 cm. H₂O in resting, healthy specimens. The pressure in the dorsal vessel during its most relaxed phase still exceeded atmospheric pressure by 5–10 cm. H₂O. The dimensional changes in the vessel during a peristaltic contraction were considerable and an almost complete emptying of the dorsal vessel was effected by a peristaltic contraction (Pl. 2).

The actual volume propagated by one complete peristaltic contraction must be sizable in an animal as long as *G. giganteus*. The diameter of the dorsal vessel as depicted in Pl. 1 was approximately $\times 3$ natural size. The velocity of the propagated

contraction can be inferred from the same figure. A value of 12 segments per second at a room temperature of 18° C. is much higher than the 1.3 segments per second reported by Haffner for a species of *Lumbriculus*. His figure was estimated from visual observation of a live animal. The present radiographs were taken in segments 50-70 and do not provide evidence as to whether the peristalsis moves at a uniform speed along the entire length of the animal.

It has been vigorously debated whether other vessels than the dorsal vessel are rhythmically pulsating in earthworms. Most authors express the opinion that the vessels connected to the dorsal vessel also possess an inherent rhythmical pulsation. The data presently obtained from the radiological analysis may throw some light on this problem. The chief vessels connected to the dorsal vessel are the parietals and dorso-intestinals. Most workers have assigned opposite functions to these vessels, one set being collecting vessels emptying into the dorsal vessel, the other being distributing vessels from the dorsal vessel. Johnston & Johnson (1902) take exception to this and maintain that both types of vessels are afferent to the dorsal vessel. The angiograms (Pl. 2), delineate only one set of vessels per segment. However, plastic injections of the dorsal vessel clearly reveal two sets in addition to the small dorso-typhlosolar vessels entering in a strictly ventral aspect. The angiograms hence suggest that when only one set of vessels is filled with contrast medium from the dorsal vessel such vessels must be naturally efferent. Successive frames also demonstrate a passage of contrast away from the dorsal vessel in these vessels. The reservation should be made that the pressure from the contrast injection may have impaired valve action in these vessels and filled them in the retrograde direction. But if so it would imply that the valves in the other vessels were more competent and this seems unlikely. It is quite possible, however, that significant species differences occur.

The relative ease with which the frequency of dorsal vessel peristalsis can be observed visually in many earthworms, has led to several publications on the subject. A direct comparison of these figures, as well as their dependence on temperature, etc., are of only limited value as the experimental conditions, and previous history of the animals used in the various studies, are unknown. What seems to have an obvious physiological significance is the large variability observed in individual specimens in the frequency of the dorsal vessel peristalsis. Nothing is known about possible factors other than temperature that could account for such variations. Suggestive evidence from the present study justifies the assumption that the load or degree of filling of the dorsal vessel may be a determinant for the frequency as well as the force of contraction of the peristaltic waves.

Most earlier authors share the opinion that the frequency of contraction of the dorsal vessel is identical with that of the lateral hearts, their contraction simply being a continuation of the former (Biedermann, 1904, Stübel, 1909, Stephenson, 1930, Haffner, 1927). Haffner states that the commissural hearts contract in complete synchrony and harmony with the dorsal vessel peristalsis, and Aoki (1930) sees no functional differentiation between the hearts and the dorsal vessel. The results reported here for *Glossoscolex* are indisputably at variance with this. The dorsal vessel peristalsis was always much lower in frequency than the contractions of the hearts regardless of whether the latter were in synchrony or not. Prosser and Zimmerman (1943) similarly reported no correspondence between the beat of the dorsal vessel and that of the

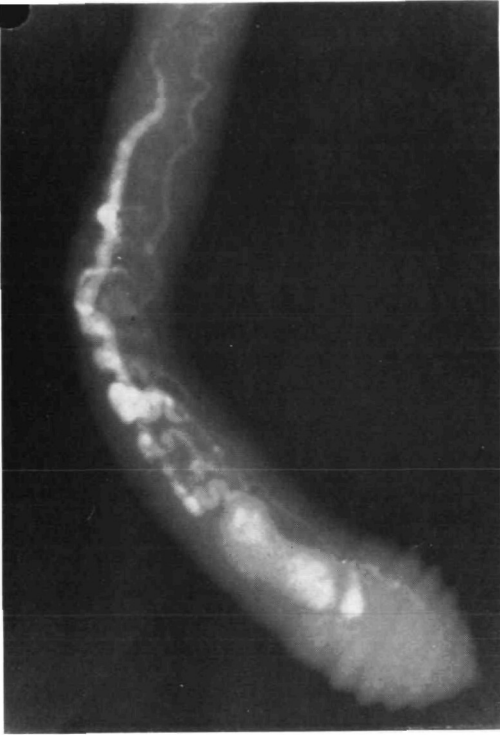
hearts in *Lumbriculus*. They noted that usually the hearts beat faster and more irregularly than the dorsal vessel. The problem of how five pairs of hearts spaced in parallel and filled from the same vessel can display a perfectly concerted and synchronous contraction is very challenging. A co-ordination based on one central pacemaker seems unlikely. A neurogenic co-ordination as suggested by Prosser *et al.* (1950) for hearts of annelids in general, but not proven, may seem the best fitted for such a task. However, here again the initiation of contraction should be such as to insure optimal filling of all the consecutive pairs of hearts at the same time. This may seem impossible to obtain since they are filled successively. However, there is an obvious decrease in size of the hearts as one moves anteriorly. This fact offers a structural basis for more uniform filling and distension of the contractile elements as the posterior and largest hearts are favoured by better filling. That the synchronous contraction of all the hearts can be easily disturbed was amply documented in the present study. It was also revealed that a concerted contraction gave substantially higher and more uniform levels of pressure in the ventral vessel. It remains possible that the small worms, most advantageous for visual study, require and show a lower frequency of heart contraction.

The present data offer conclusive evidence that the force of contraction of the lateral hearts within limits depends on their end-diastolic volume or distension. The general validity of the Starling concept for a contracting heart has thus been extended to include the specialized and unique system of hearts in oligochaetes. It merits attention that changes in the force of contraction of the hearts mediated by fluctuations in return of blood occurred spontaneously in free-moving specimens, thus proving a normal regulatory effect of the response.

The energy released by the hearts and the consequent levels of pressure reached in the ventral vessel were considerably higher than expected. The peripheral resistance was kept high, as must be assumed if proper distribution of blood to the hind portions of the body is to be possible at all. The interaction of the hearts and the vasomotor system maintained a substantial diastolic pressure. This pressure provides for a continuous perfusion of capillary beds, like those in the skin and intestines, where essential exchange and absorptive processes take place. The ventral vessel was of a considerably smaller calibre than the dorsal. Its muscular elements were well developed, presumably to hold the sizable pressures and to execute vasoactive adjustments. There was never any peristaltic activity apparent in the ventral vessel.

Prosser *et al.* (1950), quoted by Laverack (1963), reported that pressures in the vessels of *Lumbricus* were always very low, ranging from 4.4 to 5.5 mm. Hg when the animal was at rest to something more than 9.3 mm. Hg when active. There is no reference to methods or what vessel or vessels the measurements have been made on. Their values are certainly at variance with those obtained on the giant earthworm *Glossoscolex giganteus*.

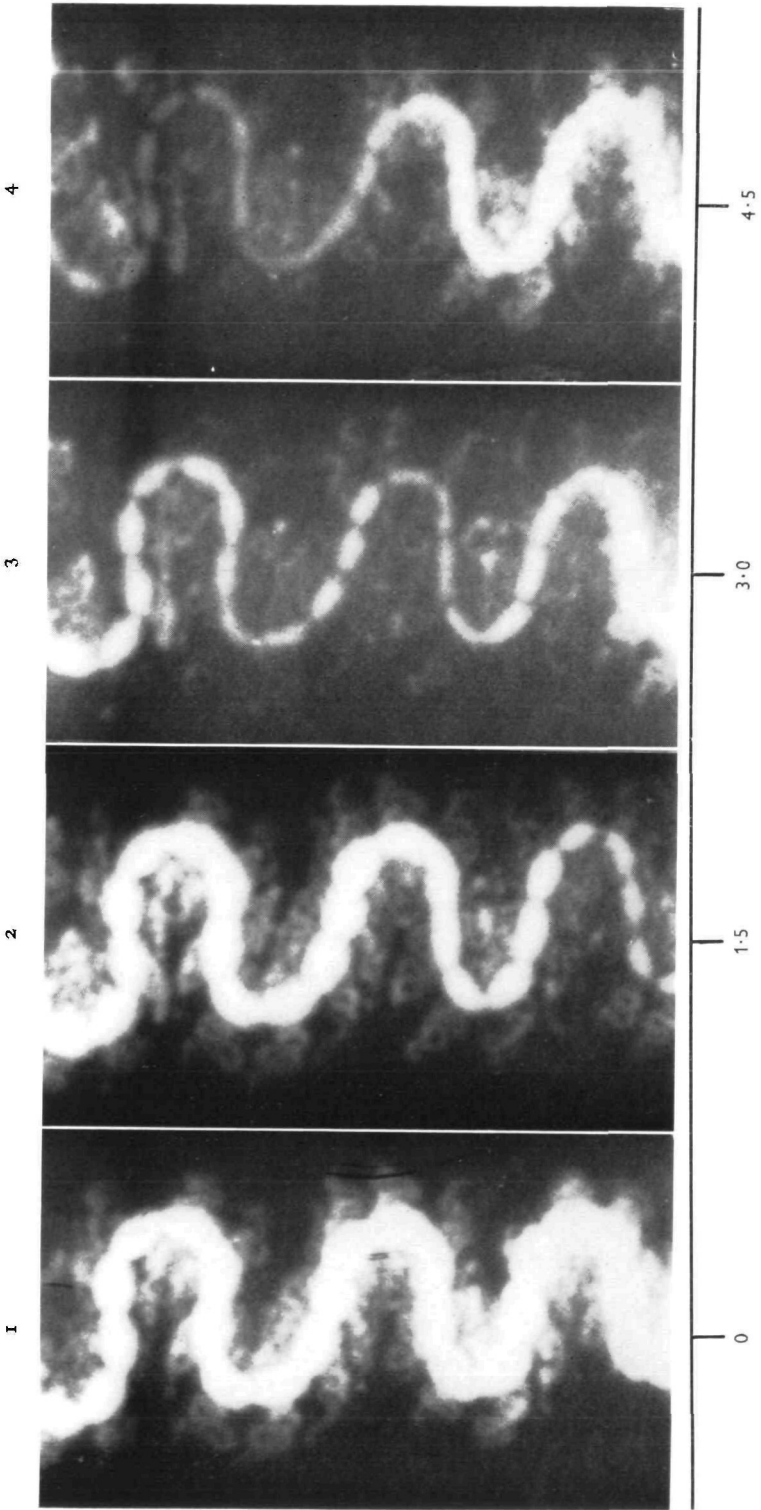
The records of pressure obtained during normal movement and digging in soil demonstrates that the general body musculature has a dramatic effect on the levels of pressure. In many invertebrates muscular activity is known to provide changing internal pressure gradients that bring about random movement of blood or coelomic fluid (Chapman, 1958). In the earthworm, however, the effects of general muscular movements are only superposed on the already sizable pressures inherent to the cardiovascular system and thus influence the general course of circulation only in degree.



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K. JOHANSEN AND A. W. MARTIN

SUMMARY

1. Intravascular pressures and angiographic records have been made on the giant earthworm, *Glossoscolex giganteus*. The measurements were made on unanaesthetized animals after previous implantation of indwelling catheters.

2. The pressures developed by the peristaltic activity of the dorsal vessel showed an average systolic value of 24 cm. H₂O while the diastolic value was 14 cm. H₂O. The frequency was variable around 6–8 contractions per min.

3. Angiographic analysis showed the peristaltic activity to include about 25 segments and to move at a velocity of 12 segments per second at 18° C. The lumen of the dorsal vessel was almost fully constricted during peristalsis.

4. The peristaltic activity of the dorsal vessel was responsible for the filling of the lateral hearts. These in turn showed an increased force of contraction at each peristaltic contraction.

5. The five pairs of lateral hearts usually contracted in synchrony. Their frequency of contraction was considerably higher than the peristalsis of the dorsal vessel (20 beats per min.).

6. The pressures developed in the ventral vessel in response to the lateral heart contractions were considerable and exceeded 100 cm. H₂O during vigorous activity. All intravascular pressures were markedly increased by general motor activity of the earthworm.

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EXPLANATION OF PLATES

PLATE 1

Successive roentgen frames demonstrating the passage of contrast medium injected into the dorsal vessel. Temperature 18–20° C. Exposures done at 50 kV. Exposure rate 0.03 sec.

PLATE 2

Roentgen frames showing the propagation of a peristaltic contraction in the dorsal vessel of an earthworm. Time scale in seconds at the bottom. Temperature 18–20° C. Exposures done at 50 kV. Exposure rate 0.03 sec.