

THE BLOOD-VASCULAR SYSTEM OF THE EARTHWORM *LAMPITO MAURITII* (KINB.).

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INTRODUCTION.

Students of Indian Zoology are greatly indebted to Dr. K. N. Bahl for his valuable contributions on the anatomy and development of *Pheretima*. *Pheretima*, however, is a type studied in the North Indian Universities, and also in Calcutta and Bombay ; and students of Zoology in South India have long felt the need for a complete and accurate account of the anatomy of *Lampito mauritii* (Kinb.) which is the type studied by them. To meet this long felt want, a complete study of the anatomy of *Lampito mauritii* was undertaken at the suggestion of Mr. R. V Seshaiya.

The present account deals with the blood-vascular system, and it is hoped that accounts of the other systems will be published in due course.

My best thanks are due to Dr. K. N. Bahl who was kind enough to go through the manuscript and make very helpful criticisms and suggestions, and to Mr. R. V Seshaiya for guidance and valuable suggestions. I am also thankful to Dr. S. G. Manavalaramanujam, Professor of Zoology, Presidency College, Madras, for the interest he took in my work and for sending me some of the references.

PREVIOUS WORK.

In a recent paper on the circulation of *Octochaetus thomasi*, Bleakly (1935) has given a good summary of previous work on the blood-vascular system and circulation in Earthworms. The works of Bourne (1891) on *Megascolex coeruleus*, Johnstone and Johnstone (1902) on *Lumbricus* (summarised by Bleakly), Bahl (1921) on *Pheretima*, Bleakly (1935) on *Octochaetus*, and Stephenson (1930) on Oligochaeta in general have been very useful to me in connection with my investigations. Besides giving as far as possible an adequate account of the blood system in *Lampito mauritii*, I have enumerated the differences in the blood-vascular system between *Lampito mauritii* and the genera above mentioned.

METHODS.

The methods given by Bahl (1921) were adopted for the study of the blood-vascular system. Dissections of the animal were made from the dorsal, ventral and lateral surfaces in physiological salt solution, and the blood-vessels were traced with great care under a dissecting binocular microscope. As even the major blood vessels are minute, injection with coloured fluid could not be carried out. Dissections were supplemented with a study of the transverse sections through the different regions of the body.

To study the disposition of the plexuses in the wall of the gut, the narcotised animal was first fixed in Bouin, and then opened under water,

The alimentary canal was slit open and the contents removed by a thorough washing. Small portions of the gut-wall were then removed and washed in very dilute KOH, dehydrated, and mounted as suggested by Bahl (1921).

To ascertain the course of circulation, very small worms were selected, and examined alive under a dissecting binocular microscope. The course of circulation was visible through the delicate body-wall in the case of the pulsating vessels *viz.*, the dorsal vessel and the hearts. The observations recorded show that the flow in the dorsal vessel is from behind forwards, and in the hearts from the dorsal to the ventral vessel.

The flow in the non-pulsating vessels was studied by the method described below. Live worms were cut open and pinned to a board. While viewing through the binocular dissecting microscope, the ventral vessel was cut behind the hearts. Profuse bleeding was seen from the cut end which was towards the region of the hearts. This shows the great pressure on this side, and explains also, that the flow of blood in the ventral vessel is backwards behind the hearts. By cutting the ventral vessel immediately in front of the hearts it was seen that the flow was forwards in this region. Similarly, when the ventro-tegmentaries and ventro-intestinals were cut, the flow was observed to be from their proximal ends, thereby showing, that blood flows through them from the ventral vessel. When the dorso-tegmentary vessels are cut, the flow is from the distal end, which indicates that blood flows through these vessels from the integument into the dorsal vessel. In the case of the dorso-intestinals, this method could not be adopted owing to their very small size; they were studied only in transverse sections.

Description of the blood-vessels.

As in the case of all earthworms, in *Lampito mauritii* there is considerable difference between the blood-vessels of the anterior region and those of the intestinal region. Behind segment XIII, the arrangement of the blood-vessels is simple, typical and uniform in all segments. But in the anterior segments, where all the important organs of the animal lie, the arrangement is different. The account of the vascular system may be dealt with under three heads:—

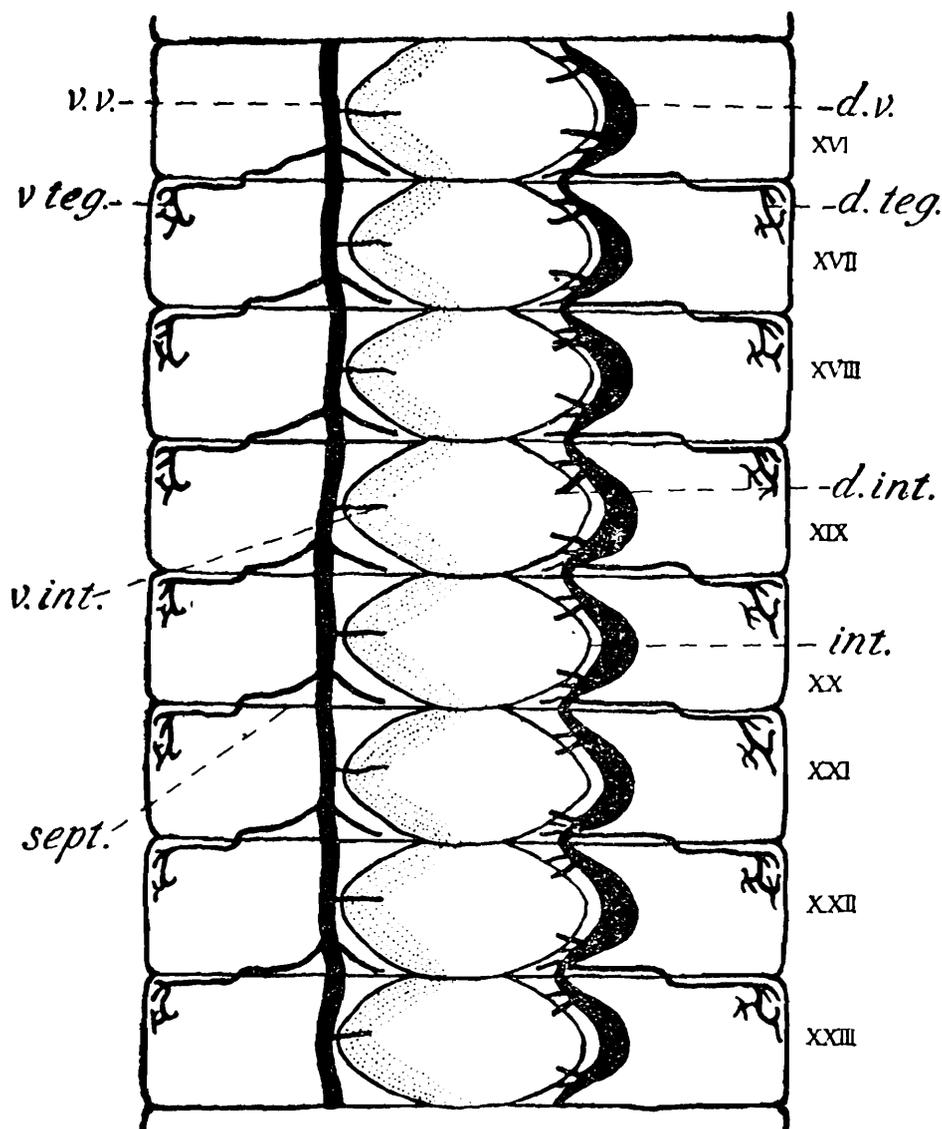
- (A) The blood-vessels behind segment XIII.
- (B) The blood-vessels of the anterior region.
- (C) The course of circulation of the blood.

A. The blood-vessels behind segment XIII—the typical arrangement.

The blood-vessels in this region some of which are not exclusively confined to this region include the following:—(1) the dorsal vessel (2) the dorso-tegmentaries (3) the dorso-intestinals (4) the ventral vessel (5) the ventro-tegmentaries (6) the ventro-intestinals (7) the intestinal plexus and (8) the parietal vessels. Of these, the dorsal vessel, the ventral vessel, and the parietal vessels extend into the anterior region also and are therefore not exclusively characteristic of this region. There are no sub-neural and sub-intestinal vessels in *Lampito mauritii*.

(1) *The Dorsal vessel.*—The dorsal vessel, as its name indicates, lies dorsal to the gut, and extends from one end of the animal to the other.

It is the central contractile vessel from which blood is sent to the different parts of the body through vessels having direct communication with it.



TEXT FIG. 1. Lateral view of eight segments (XVI to XXIII) of the intestine presenting the arrangement of the blood vessels of that region.

d.int. dorso-intestinals; *d.teg.* dorso-tegmentary; *d.v.* dorsal vessel; *int.* intestine; *sept.* septum; *v.int.* ventro-intestinal; *v.teg.* ventro-tegmentary. *v.v.* ventral vessel.

It passes through the successive intersegmental septa all along its course. Between every two successive septa, *i.e.*, in the segmental region, it is swollen, but in the passage through the septa it is very much narrowed. The structure of the dorsal vessel in the anterior region is different from that behind segment XIII and will be described later on. Behind segment XIII the dorsal vessel receives branches from the intestinal-wall and body-wall and has no hearts connected with it.

From the intestine the dorsal vessel receives in each segment two pairs of small vessels called the *dorso-intestinals*, and from the integument a pair of fine vessels in each segment called the *dorso-tegmentaries*. Posteriorly in the anal region the dorsal vessel arises from minute branches which ramify into the integument, and some of them get connected with similar minute branches of the ventral vessel.

(2) *The Dorso-tegmentaries*.—There is a pair of these in each segment arising from the body-wall and joining finally the dorsal blood-

vessel. They return blood from the body-wall to the dorsal blood vessel. Each dorso-tegmentary arises by the union of minute branches from the body-wall, and runs along the posterior face of the septum to its middle part, where it pierces the septum and enters the next preceding segment. Here it runs on the anterior face of the septum and finally joins the dorsal vessel at the point of its septal constriction. At the junction of the dorso-tegmentaries with the dorsal vessel, valves are present which allow the flow of blood from the dorso-tegmentaries into the dorsal vessel but not in the opposite direction.

(3) *The Dorso-intestinals*.—These vessels serve to carry the blood from the wall of the alimentary canal to the dorsal blood vessel. Two pairs of these found in each segment join the dorsal vessel in the middle of the segment. They arise from branches in the wall of the intestine and run to the dorsal vessel into which they open. At the point of their junction with the dorsal vessel there are valves which allow the flow of blood into the dorsal vessel but not from the latter into the dorso-intestinals.

(4) *The Ventral vessel*.—This is a longitudinal vessel running from one end of the animal to the other and lying ventral to the alimentary canal from which it is suspended by the mesentery. It is of a uniform thickness throughout, except in the anteriormost region where it narrows considerably. Its structure and origin in the anterior region will be described in detail under the blood-vessels of the anterior region.

At the posterior end of the animal the ventral vessel breaks up into minute branches some of which are connected, as pointed out before, with similar branches of the dorsal vessel. In the anterior region, as will be seen later on, it receives the lateral hearts but in the intestinal region it gives off in each segment a pair of *ventro-tegmentaries* to the integument, and a single, fine vessel, the *ventro-intestinal*, to the wall of the intestine. The ventral vessel is non-contractile and has no valves.

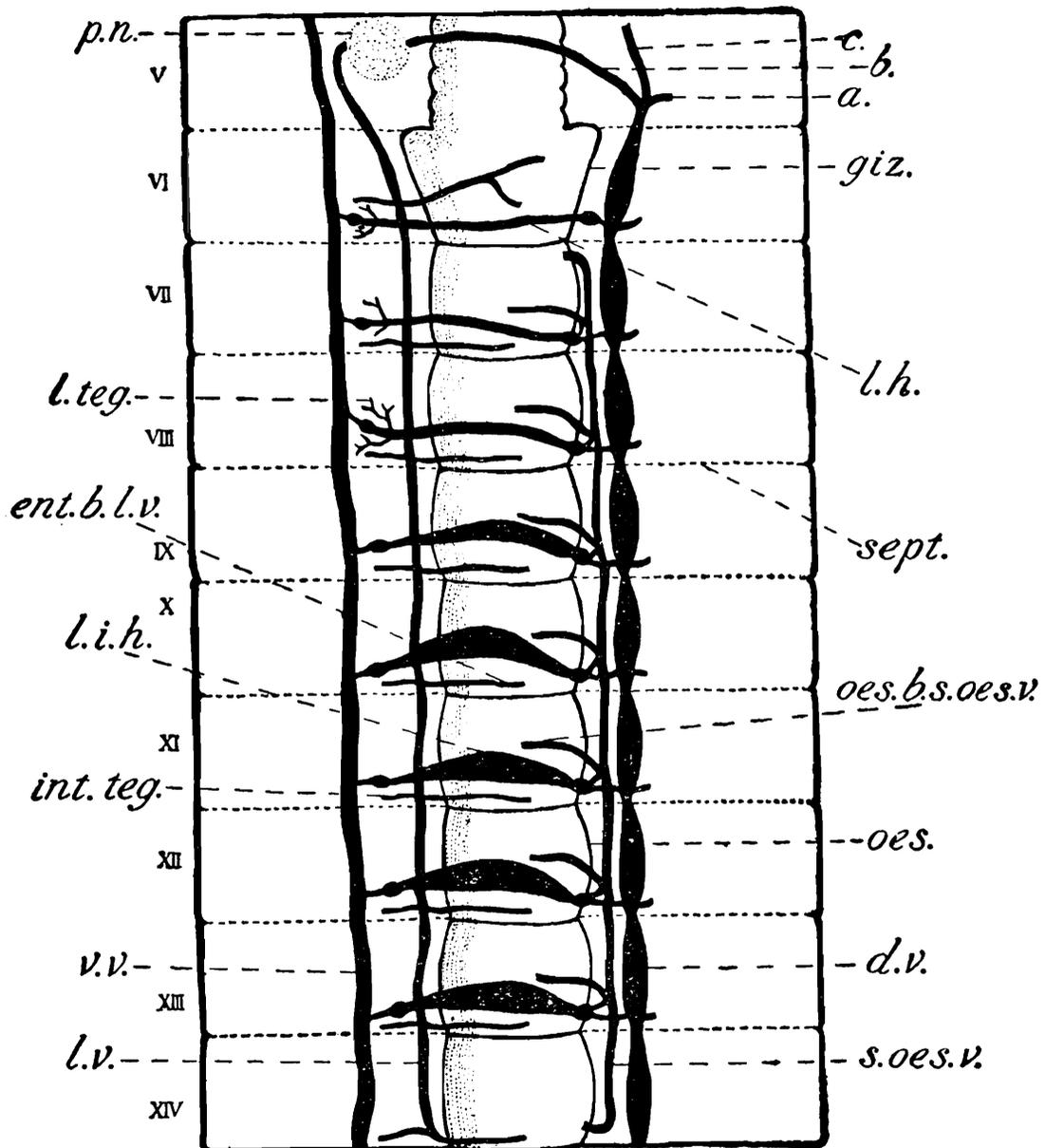
(5) *The Ventro-tegmentaries*.—These carry blood from the ventral vessel to the body-wall. They are paired vessels, arising posteriorly in each segment from the ventral vessel, and proceeding towards the middle of the posterior septum of the segment where they run on its anterior surface. Then they pass through the septum and enter the succeeding septum, where they run along its posterior face and finally end in capillaries in the body-wall. The ventro-tegmentary vessel in segment XVIII gives off a fine branch to the prostate gland.

(6) *The Ventro-intestinals*.—The ventro-intestinal is a minute, single vessel in each segment serving to carry the blood from the ventral vessel to the intestine. It arises from the ventral vessel about the middle of each segment and runs to the wall of the intestine. There are no valves in the ventro-intestinal vessel.

(7) *The Intestinal plexus*.—The intestinal plexus is situated between the epithelial and muscular layers of the gut-wall. It consists of a very fine anastomosing net-work of capillary vessels having the general appearance of a sinus running all round in the intestinal-wall.

(8) *The Parietal vessels*.—These are paired vessels lying one on either side of the alimentary canal and extending over six segments *viz.* XIII

to XVIII. They usually originate from eight minute branches in the body-wall in segments XIV to XVII and, running forwards, open into the lateral oesophageal vessels in segment XIII. In addition to the branches from the body-wall the parietal vessel of each side receives in segment XVIII a pair of fine branches from the prostate glands. In the middle of segments XV, XVI and XVII the parietal vessel of each side gives off a branch to the ventral wall of the intestine which divides into three before running up the wall of the intestine.



TEXT FIG. 2. Lateral view of *Lampito mauritii* from segments V to XIV, showing the arrangement of the blood vessels in that region.

a., *b.* and *c.* anterior branches of the dorsal vessel; *d. v.* dorsal vessel; *ent. b. l. v.* enteric branch of the lateral oesophageal vessel; *giz.* gizzard; *int. teg.* intestino-tegumentary; *l. h.* lateral heart; *l. i. h.* latero-intestinal heart; *l. teg.* latero-tegumentary; *l. v.* lateral oesophageal vessel; *oes.* oesophagus; *oes. b. s. oes. v.* oesophageal branch of the supra-oesophageal; *p. n.* pharyngeal nephridia; *sept.* septum; *s. oes. v.* supra-oesophageal vessel; *v. v.* ventral vessel.

B. *The blood-vessels of the anterior region* (Segments I to XIII).

The blood vessels of the anterior region include (1) the dorsal vessel (2) the hearts and the latero-tegumentaries (3) the lateral oesophageal vessels (4) the ventral vessel (5) the supra-oesophageal vessel and (6) the

oesophageal plexus. Of these, as stated already, the dorsal and ventral vessels are common to the anterior and posterior regions: We have also seen that the parietal vessels extend into segment XIII. All the remaining vessels are peculiar to the anterior region.

(1) *The Dorsal vessel*.—The main disposition of the dorsal vessel has already been described. In some of the Megascolécidae the dorsal vessel is double, but in *Lampito mauritii* it is single. From segment VII forwards it is more or less narrow, and in the region of the gizzard it divides into three branches, one median and two lateral. The median branch proceeds forwards and divides into minute branches supplying the body-wall and the tissue surrounding the buccal cavity. The lateral branches, on the other hand, become connected with ventro-laterally placed longitudinal vessels known as *lateral oesophageals* on either side through the pharyngeal nephridial tufts in segment V. The dorsal vessel is the main contracting vessel, and the flow of blood in it is from behind forwards.

The dorsal vessel in the anterior region does not receive any vessels from the body-wall or intestine, but is connected with the hearts.

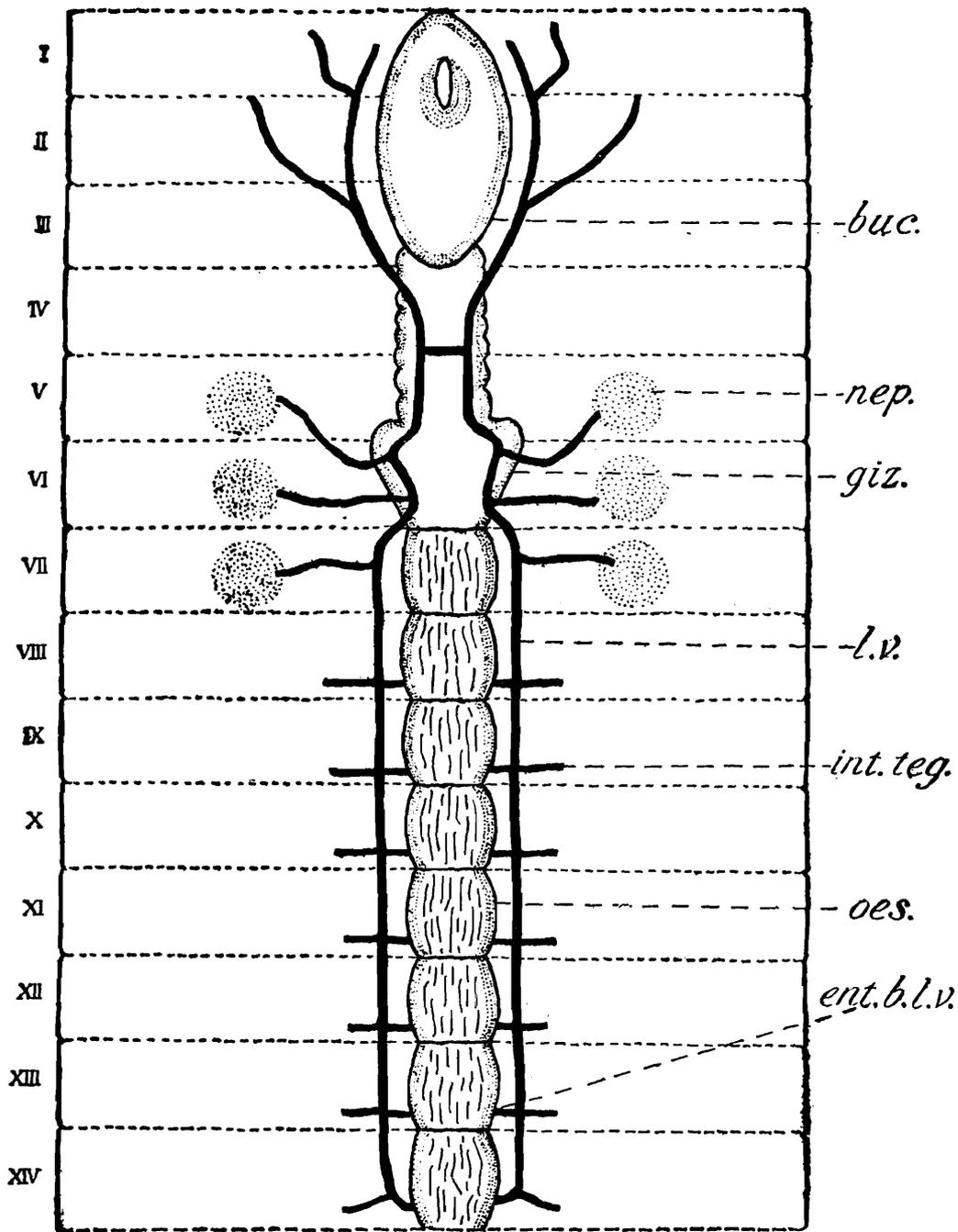
(2) *The Hearts and the Latero-tegmentaries*.—The hearts are paired contractile vessels found on the sides of the alimentary canal connecting the dorsal and the ventral vessels. There are altogether eight pairs of hearts, a pair in each of the eight segments, VI to XIII. Gates (1938) states that there are only four pairs of hearts, those in segments VI to IX being merely commissural vessels. But I have observed the contraction of all the eight pairs of vessels, and have no doubt that they are all contractile hearts. The anterior four pairs of hearts are thinner and longer than the posterior four pairs. The first pair of hearts encircles the gizzard. The remaining pairs arise dorsally by two roots, one from the dorsal vessel and the other from the supra-oesophageal vessel. Of the eight pairs of hearts, therefore, the first pair are the *lateral hearts* and the remaining seven pairs are the *latero-intestinal hearts*. The opening of the latero-intestinal heart into the supra-oesophageal vessel is close to that of the oesophageal vessel which runs up from the oesophageal plexus to the supra-oesophageal.

The two ends of each heart, and the dorsal connection with the dorsal vessel as well as the ventral connection with the ventral vessel are narrow. Close to either narrow end there is a bulbous dilatation of the heart.

The first three pairs of hearts, before they reach the ventral vessel close to the ventral bulbous dilatations, give off to the nephridia, the body-wall, and the spermathecae branches which may be called the *latero-tegmentaries*. These represent the *ventro-tegmentaries* of the anterior region of some authors. Since these arise from the lateral and latero-intestinal hearts and not from the ventral vessel I consider it appropriate to name them *latero-tegmentaries*. The remaining five pairs do not give off these branches.

(3) *The Lateral Oesophageal vessels*.—These are paired longitudinally disposed vessels extending from segment II to segment XIV and lying nearer the ventral side of the alimentary canal. Anteriorly they arise in the region of the buccal cavity in segment II by two minute branches on either side. In segment III each lateral oesophageal is joined by

another branch which comes from the nephridium of that segment. In segment V the two lateral-oesophageal vessels come to lie side by side on the ventral surface of the oesophagus and are connected by a transverse vessel. In segment XIV they end in a plexus on the wall of the



TEXT FIG. 3. Ventral view of *L. mauritii* from segments I to XIV, showing the disposition of the lateral oesophageal vessels and their branches.

buc. buccal region; *ent. b. l. v.* enteric branch of the lateral oesophageal vessel; *giz.* gizzard; *int. teg.* intestino-tegumentary; *l. v.* lateral oesophageal vessel; *nep.* nephridia; *oes.* oesophagus.

oesophagus. All along their course these two vessels receive branches from the body-wall and nephridia, which are called the *intestino-tegumentary* vessels of the anterior region, and give off branches to the oesophagus. The branch to the oesophagus lies in the posterior part of each segment.

Bahl (1921) has described in *Pheretima* these lateral oesophageal vessels as being the forward continuations of the sub-neural vessel which

forks at its anterior end in segment XIV. These branches are then continued forwards, soon coming to lie along the oesophagus and communicating freely with the oesophageal vessels in its wall.

Bourne (1891) adds that they are specializations of the intestino-tegumentary system. They begin anteriorly in a net-work on the pharynx with which the dorsal and ventral vessels are also connected, and end behind on the alimentary tube; they receive segmental branches from the septa, parietes and nephridia, and give off branches to the alimentary canal.

Beddard (1895) holds them to be homologous with the sub-intestinal, a double sub-intestinal, and therefore as specializations of the alimentary plexus.

In *Lampito mauritii* the sub-neural vessel is absent. The condition noticed in this species lends support to Bourne's suggestion, that the lateral oesophageals are specializations of the intestino-tegumentary system. The lateral oesophageal vessels of this form may be considered as specializations of the intestino-tegumentary system, since these two vessels are connected directly with the integument and the alimentary canal. The lateral oesophageal vessels apparently serve for the return of blood from the anterior region.

(4) *The Ventral vessel*.—It has been said already that the ventral vessel is a main non-contractile vessel running from the anterior end to the posterior end of the animal. It lies ventral to the alimentary canal, suspended from it by the mesentery, and is of a uniform thickness except in the anteriormost region where it narrows considerably. Anteriorly, in segment I the ventral vessel originates by the union of two main roots which in their turn are formed out of more minute branches. Some of the latter are connected dorsally with minute branches of the dorsal vessel.

In the region in front of segment XIV the ventral vessel gives off no branches to the integument and gut-wall. It receives however the eight pairs of hearts described already.

The flow of blood is forwards in the ventral vessel in this region.

(5) *The Supra-oesophageal vessel*.—This is a single vessel lying dorsal to the intestine and beneath the dorsal vessel, and extending from segment VII to segment XIV. It is of a uniform thickness throughout and possesses no valves. It arises in segment VII by the union of two branches coming from either side of the oesophagus. All along its course it receives a pair of branches from the oesophageal wall, running in the middle of each segment. It has already been seen that in addition to these, it is connected with the latero-intestinal hearts by a pair of branches in each of the segments VII to XIII. These two kinds of branches are connected with the supra-oesophageal close together. The oesophageal branches are afferent and take blood from the oesophagus into the supra-oesophageal, while the branches connected with the hearts are efferent and serve to carry blood into the heart from the supra-oesophageal.

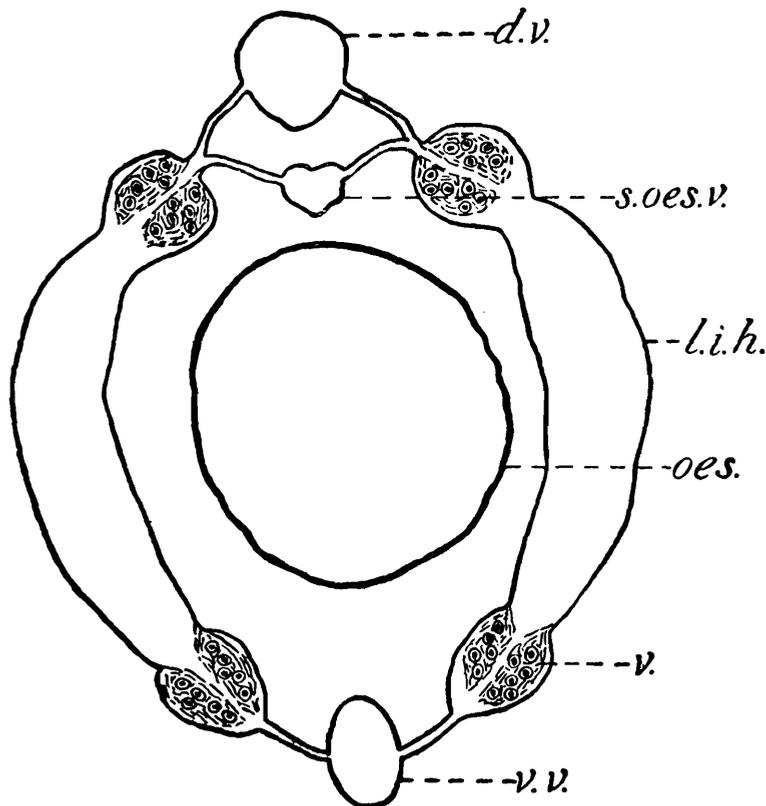
The branches from the oesophagus establish a connection between the oesophagus and the supra-oesophageal which may therefore be regarded as a specialization of the oesophageal plexus.

(6) *The Oesophageal plexus.*—This is found in the oesophageal wall between the muscular and epithelial layers extending from segments VII to XIV. It consists of a very fine and closely set net-work of capillaries, having in transverse sections of the oesophagus the appearance of a sinus running all round in the oesophageal wall. The oesophageal lining is produced into a number of finger-shaped or villi-like processes, and the oesophageal plexus extends also into these processes.

Valves.

As mentioned already, valves are present in the dorsal vessel, the lateral and latero-intestinal hearts, the dorso-intestinals, and the dorso-tegumentaries.

The valves are of two kinds (1) double-valves occurring in the hearts and (2) single circular-valves occurring in the dorsal vessel, dorso-tegumentaries, and dorso-intestinals.



TEXT FIG. 4. Transverse section passing through a pair of latero-intestinal hearts with the dorsal and ventral connections showing the valves. The layers of the body-wall are omitted.

d. v. dorsal vessel; *l. i. h.* latero-intestinal heart; *oes.* oesophagus; *s. oes. v.* supra-oesophageal vessel; *v.* valve; *v. v.* ventral vessel.

(1) *The Double-valve.*—This kind of valve occurs in the hearts. It is placed in the bulbous dilatation present near either extremity of the heart. Each valve consists of two pear-shaped masses of tissue with scattered nuclei placed opposite each other; each mass has one end attached to the wall of the heart, and the other freely projecting into the lumen of the heart. The attached end is near the dorsal vessel, while the free end is broad and directed away from the dorsal vessel. The valve at the opposite end of the heart also is similar, but its attachment is directed away from the ventral vessel and the free lobes are

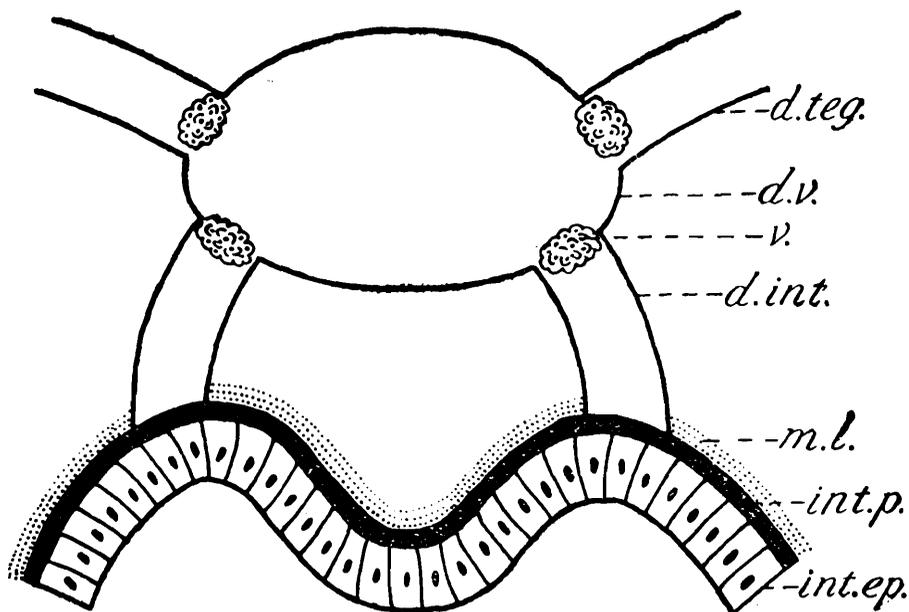
directed towards the ventral vessel. When the valves are open, they float freely in the blood stream, and when closed they meet one another and block the passage.

(2) *The Circular-valve.*—This type of valve occurs in the dorsal vessel at its septal constrictions, and at the junction of the dorso-tegmentaries and dorso-intestinals with the dorsal vessel. It consists of a mass of tissue presenting the appearance of a morula with scattered nuclei. The flap fills the entire lumen of the blood vessel at the point of its occurrence, and is attached by one end to the wall of the vessel. When the valve is open it hangs freely in the blood stream, and when closed it forms a complete transverse partition.

I was able to study the action of the valves only in the case of the hearts, the other vessels possessing valves (the dorso-tegmentaries and dorso-intestinals) being too minute for study. The flow of blood in the dorsal blood vessel, as observed in the living worm, is from behind forwards. The valves in the dorsal blood vessel allow the blood to flow only forwards. In the case of the hearts, a freshly narcotised worm was opened, and pressure applied on the heart on the side towards the dorsal vessel. Then the flow of blood down the hearts was observed. When pressure was applied on the side towards the ventral vessel there was no flow.

The course of circulation of the blood.

As in all earthworms, and as stated above, the flow of blood is forwards in the dorsal vessel, downwards in the hearts, and backwards in the ventral vessel behind the region of the hearts. Since the circulation



TEXT FIG. 5. Transverse section showing the dorsal vessel, dorso-intestinal vessel, dorso-tegmentary vessel, and the intestinal plexus. The valves present in the dorso-intestinal and dorso-tegmentary are also shown.

d. int. dorso-intestinal; *d. teg.* dorso-tegmentary; *d. v.* dorsal vessel; *int. ep.* intestinal epithelium; *int. p.* intestinal plexus; *m. l.* muscular layer; *v.* valve.

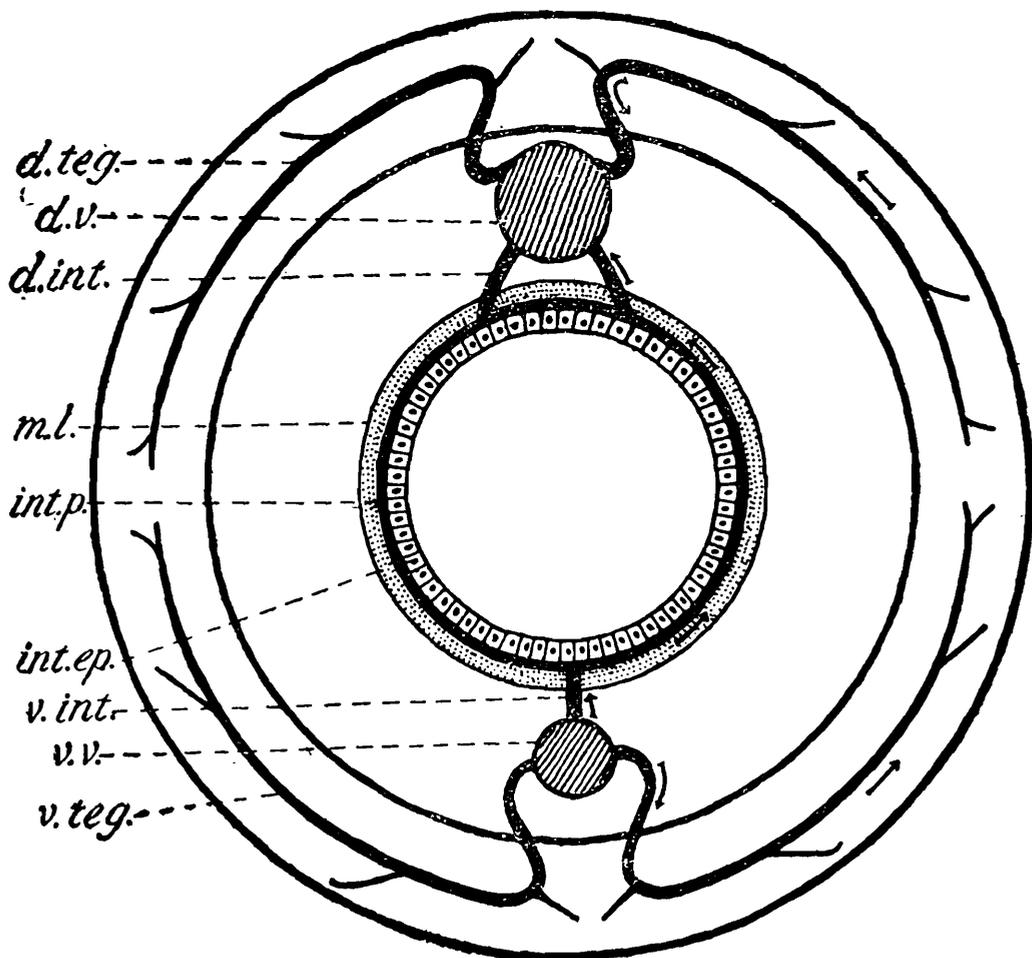
in the anterior region is different from that in the region behind, it will be convenient to deal with these two regions separately. The circulation through the parietal vessels also is dealt with separately.

1. *Circulation in the Intestinal region.*—As described already, the dorso-tegmentaries, the dorsal vessel, the dorso-intestinals, the ventral vessel, the ventro-tegmentaries, and the ventro-intestinals are the main blood vessels in this region. The course of circulation in this region was studied in the following way:—

When the dorso-tegmentary vessels are cut profuse bleeding is observed from the distal end of the cut. This shows clearly that the flow of blood in these vessels is towards and into the dorsal vessel. Moreover transverse sections show that valves are present in these vessels just at the point of their union with the dorsal vessel. These valves are disposed in such a way, that they allow blood to flow only from the dorso-tegmentaries into the dorsal vessel, but not *vice versa*.

In the dorso-intestinals, which were studied only by sections, the valves appear to allow the blood to flow into the dorsal vessel, and not from it.

Thus in the intestinal region the dorsal vessel receives blood from all the vessels connected with it.



TEXT FIG. 6. A diagrammatic sketch showing the course of circulation in the intestinal region.

d. int. dorso-intestinal; *d. teg.* dorso-tegmentary; *d. v.* dorsal vessel; *int. ep.* intestinal epithelium; *int. p.* intestinal plexus; *m. l.* muscular layer; *v. int.* ventro-intestinal; *v. teg.* ventro-tegmentary; *v. v.* ventral vessel.

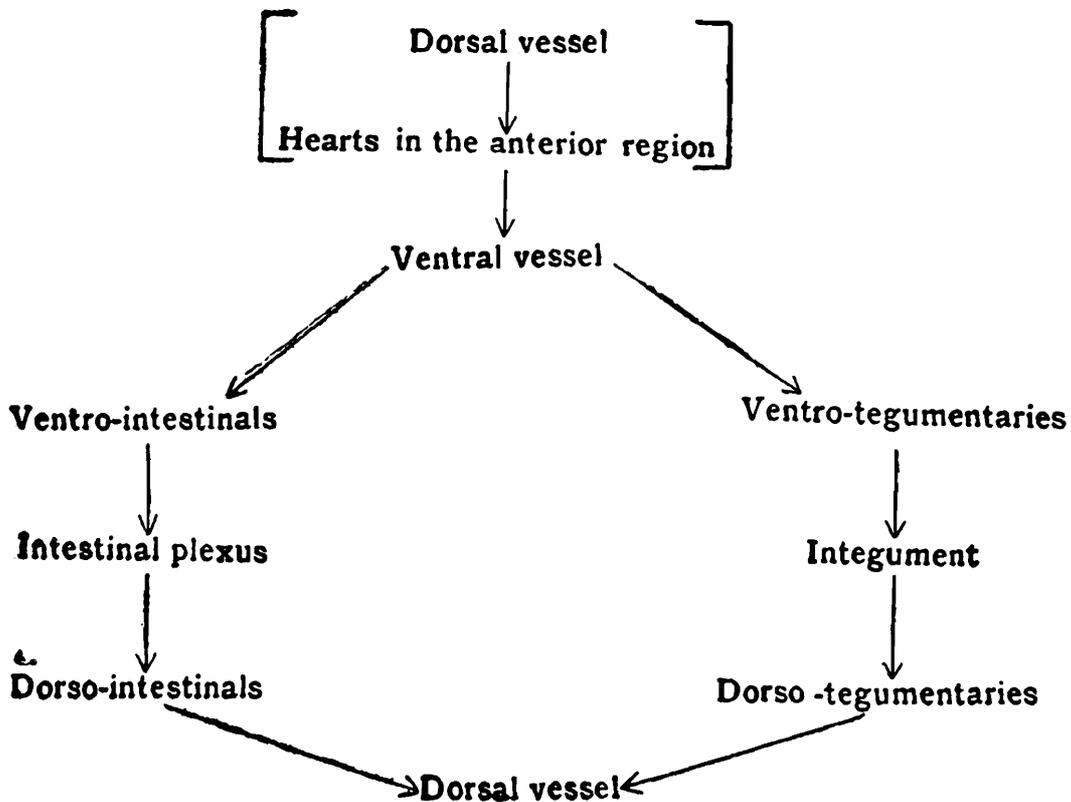
When the ventro-tegmentary vessels are cut, bleeding is observed from the proximal end of the cut, *i.e.* from the side which is attached

to the ventral vessel. The flow of blood is therefore from the ventral vessel to the tegumentary vessel.

Though the ventro-intestinal vessels are very small, it is possible to cut them. When this is done, profuse bleeding is observed from the end which is nearer the ventral vessel, and no bleeding at all from the other end. From this it is evident that blood flows from the ventral vessel into the ventro-intestinal vessel.

I was not able to study the course of circulation in the intestinal plexus. The intestinal plexus consists, as we have seen already, of a very fine close capillary net-work lying between the epithelial and muscular layers of the intestine. Since the flow of blood is from the ventral vessel to the gut-wall and from there through the dorso-intestinals to the dorsal vessel, it may be inferred that the course taken by the blood in the intestinal plexus is from the ventral side to the dorsal round the gut-wall.

To sum up, the blood from the ventral vessel in the intestinal region takes either of the following two courses:—(1) through ventro-tegu-



TEXT-FIG. 7. A diagrammatic representation of the course of circulation in the intestinal region.

mentaries to the body-wall, nephridia and from there, through the dorso-tegmentary vessels to the dorsal vessel, or (2) through the ventro-intestinals to the intestinal plexus, and from there, through the dorso-intestinals to the dorsal vessel.

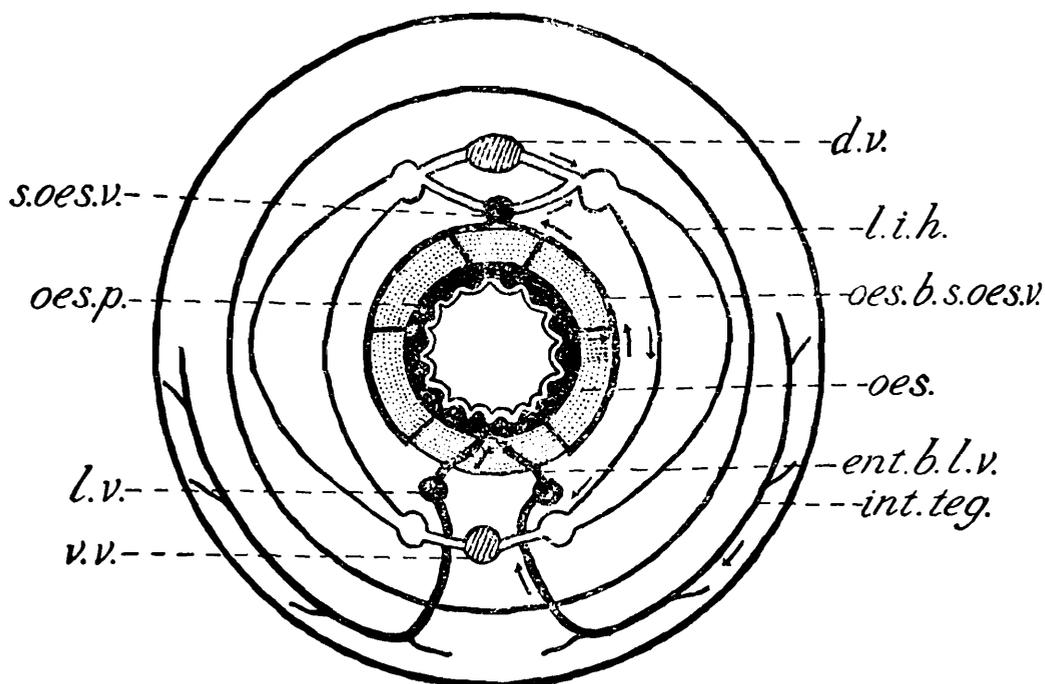
Considering the function of distributing blood to the various parts of the body, the ventral vessel and its branches are arterial, whereas the dorsal vessel and its branches, which receive blood and send it to the hearts situated in the anterior region, are venous in the intestinal region.

2. Circulation in the Anterior region (Segments I to XIII).

The arrangement of the blood vessels in the anterior region is very specialised and there is a corresponding change in the course of circulation.

In the segments anterior to XIV, as compared with what is seen in the intestinal region, there are two important peculiarities, *viz.* (1) all the vessels connected with the dorsal vessel receive blood from it, and (2) the ventral vessel communicates only with the hearts and not with other vessels.

The complete course of circulation in the anterior region is as follows:—At each contraction most of the blood in the dorsal vessel flows down the hearts to the ventral vessel. From the hearts a part of the blood passes through the latero-tegmentaries to the integument, nephridia, and spermathecae. It will be seen that the integument gets its blood, not from the branches of the ventral vessel as in the intestinal



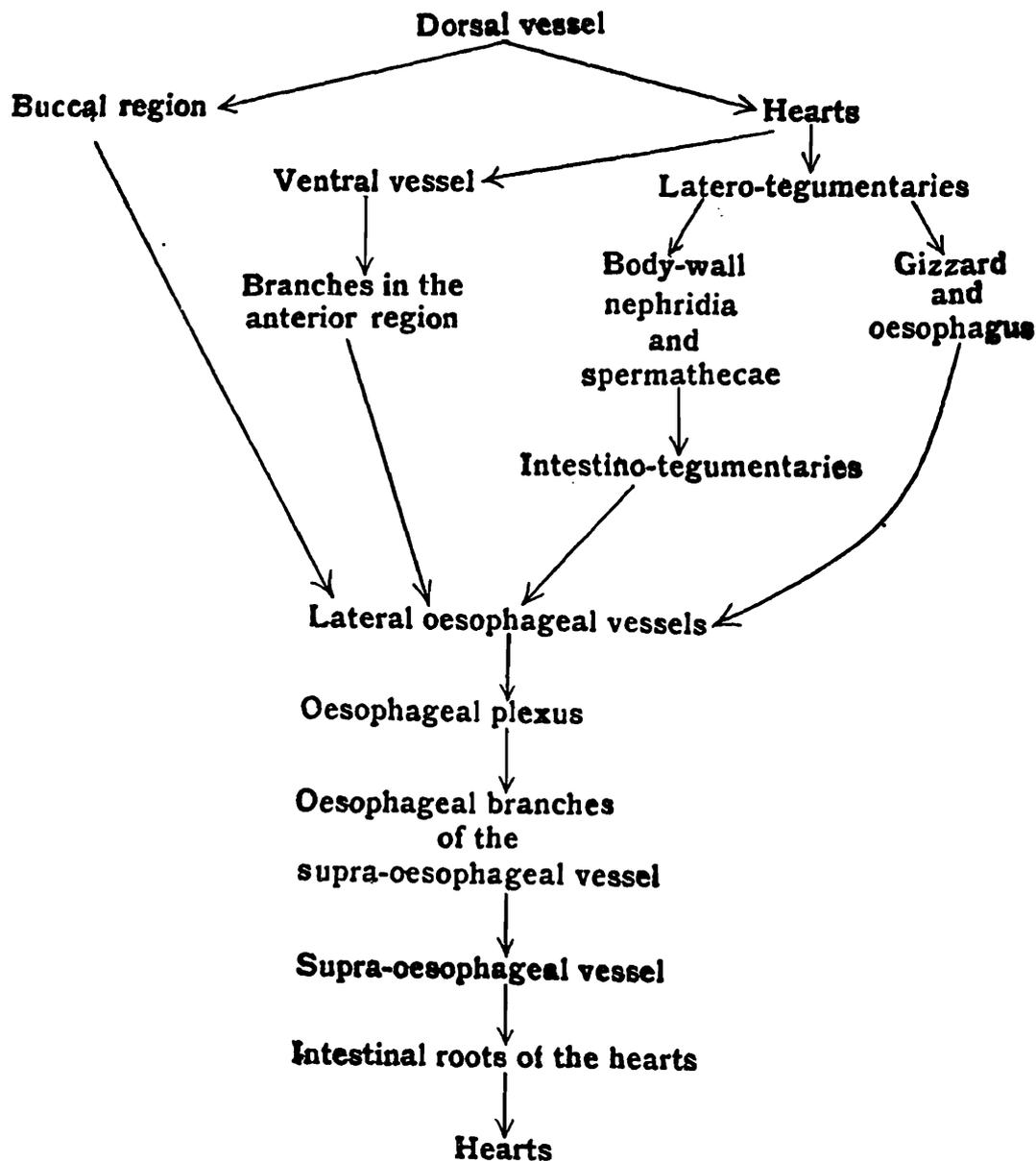
TEXT FIG. 8. A diagrammatic sketch showing the course of circulation in the region of the hearts.

d. v. dorsal vessel; *ent. b. l. v.* enteric branch of the lateral oesophageal vessel; *int. teg.* intestino-tegmentary; *l. i. h.* latero-intestinal heart; *l. v.* lateral oesophageal vessel; *oes.* oesophagus; *oes. b. s. oes. v.* oesophageal branch of the supra-oesophageal vessel; *oes. p.* oesophageal plexus; *s. oes. v.* supra-oesophageal vessel; *v. v.* ventral vessel.

region, but from the branches arising from the hearts. A part of the blood flowing in the dorsal vessel passes through a forward branch of the vessel to the buccal region.

The direction of flow in the ventral vessel is forwards in front of the hearts and backwards behind the hearts. The blood flowing forwards in the ventral vessel circulates in the capillaries of the ventral vessel in the anterior most segments, *viz.* I and II. From this region as well as from the buccal region the blood flows into the lateral oesophageal vessels in which blood flows backwards. The blood from the integument and nephridia also flows into the lateral oesophageal vessels through

the "intestino-tegmentaries" which join the lateral oesophageal vessels. Thus all the returning blood in the anterior region is gathered



TEXT-FIG. 9. A diagrammatic representation of the course of circulation in the anterior region (parietal vessels not included).

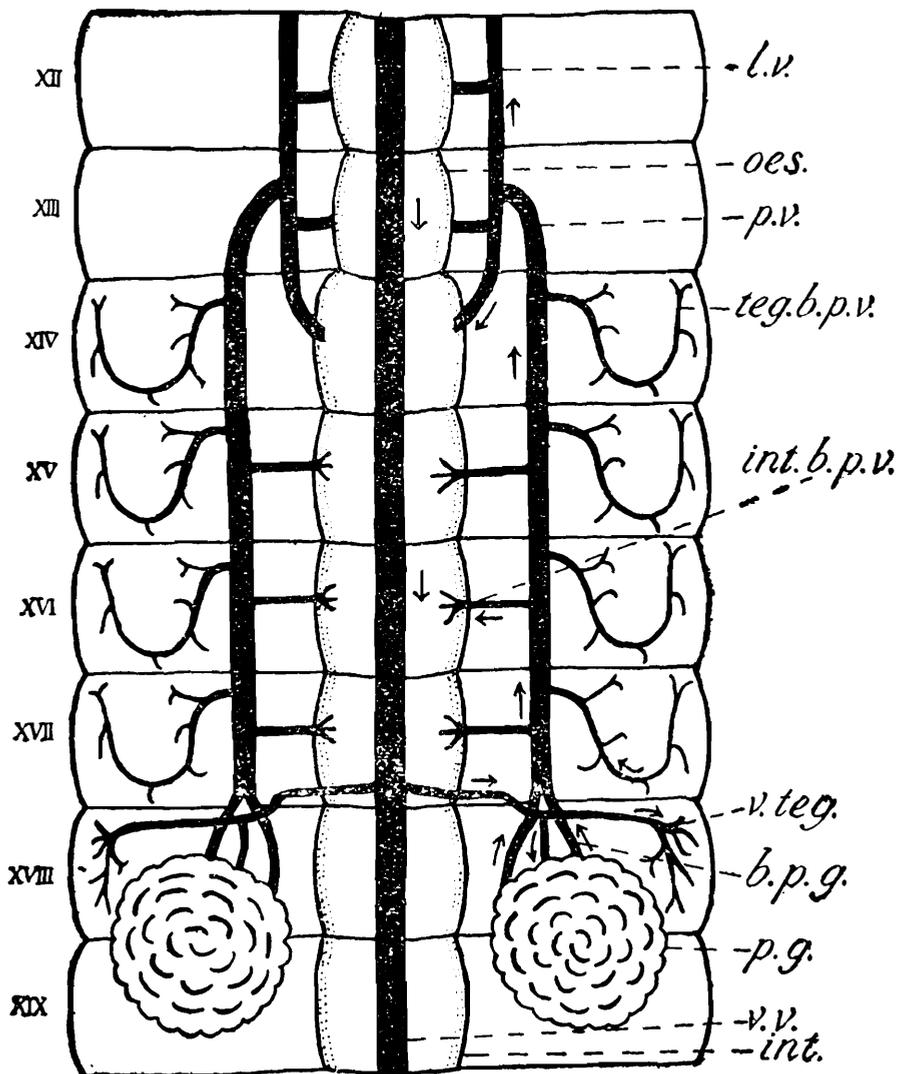
into the lateral oesophageal vessels from where it passes through the enteric branches into the oesophageal plexus which is situated in the wall of the oesophagus from segment VII to XIV

After circulating through the oesophageal plexus the blood flows through the oesophageal branches of the supra-oesophageal vessel into the supra-oesophageal vessel itself, whence it is returned into the hearts through the "intestinal" branches of the heart. In addition to the general course of circulation from the dorsal vessel to the ventral vessel and back to the dorsal vessel through the intervening vessels of the segments behind XIII, there is seen in this region a secondary passage or "short-circuit" through vessels connected with the hearts and lateral oesophageals.

3. *Circulation in the parietal vessels.*—The parietal vessels receive blood from the integument and prostate glands. From the parietal

vessels the blood takes either of the two following courses (1) through the intestinal branches of the parietal vessel into the intestinal plexus from where through the dorso-intestinals into the dorsal vessel and (2) forward into the lateral-oesophageal vessel from where it is conveyed through the enteric branch of the lateral oesophageal vessel into the oesophageal plexus, whence it is returned through the oesophageal branches of the supra-oesophageal into the supra-oesophageal vessel itself.

Comparison with other types.—With regard to the general disposition of the major blood vessels and the general course of circulation, *Lampito mauritii* agrees with forms like *Octochaetus*, *Pheretima*, and *Megascolex coeruleus*, but in the details of circulation there are several differences.



TEXT FIG. 10. Sketch showing the origin and distribution of the parietal vessels, and also the course of circulation of blood in them.

b. p. g. branch from the prostate gland; *int.* intestine; *int. b. p. v.* intestinal branch of the parietal vessel; *l. v.* lateral oesophageal vessel; *oes.* oesophagus; *p. g.* prostate gland; *p. v.* parietal vessel; *teg. b. p. v.* tegumentary branch of the parietal vessel; *v. teg.* ventro-tegumentary; *v. v.* ventral vessel.

(1) The presence of only six pairs of contractile hearts extending from segments VIII to XIII, of which four are latero-intestinal, (2) the double nature of the dorsal vessel posterior to the gizzard, (3) and the presence of the sub-intestinal vessel mark off *Octochaetus* from *Lampito mauritii*.

As compared with *Pheretima*, *Lampito mauritii* lacks (1) the "cephalic" blood vessels arising directly from the dorsal and ventral vessels, (2) the sub-neural vessel, (3) the double blood supply to the gut through a single ventro-intestinal, and also from the sub-neural through the septo-intestinal, (4) two intestinal plexuses, and (5) the commissural vessels connecting the dorsal and sub-neural vessels in each segment.

(1) In the presence of a single dorsal vessel, (2) in the possession of eight pairs of hearts, and (3) in the absence of a sub-neural, *Lampito mauritii* resembles *Megascolex coeruleus*. But in the presence of (1) a double supra-intestinal, and (2) a definite intestino-tegumentary system in each segment the latter species is strikingly different. It may also be pointed out that of the eight pairs of hearts in *Megascolex coeruleus*, the anterior three pairs are lateral hearts and the remaining five pairs are latero-intestinal hearts, while in *Lampito mauritii* there is only one pair of lateral hearts, the anteriormost, while the rest are latero-intestinal hearts.

Lampito mauritii differs widely from *Lumbricus* in the arrangement of blood vessels and in the course of circulation.

SUMMARY.

1. The blood-circulatory system of *Lampito mauritii* consists of two main longitudinal vessels, *the dorsal vessel* and *the ventral vessel*, extending from one end of the animal to the other, and of nine types of subsidiary vessels in addition to an alimentary plexus. The subsidiary vessels are (1) the supra-oesophageal vessel, (2) the lateral oesophageal vessel, (3) the hearts, (4) the dorso-tegumentaries, (5) the dorso-intestinals, (6) the ventro-tegumentaries, (7) the ventro-intestinals, (8) the intestino-tegumentaries, and (9) the parietal vessels.

2. The dorsal vessel is single and connected with the ventral vessel by eight pairs of contractile hearts, a pair occurring in each of the segments, VI to XIII. Of these the first pair are the lateral hearts and the remaining seven pairs are latero-intestinal hearts having connection dorsally both with the dorsal and the supra-oesophageal vessels.

3. The ventral vessel behind segment XIII gives off the ventro-tegumentaries to the body-wall, but in the anterior region, in segments VI, VII and VIII, the blood to the body-wall, gizzard, oesophagus, nephridia, spermathecae etc., flows through vessels which arise from the hearts and are named in this paper *latero-tegumentaries*. They correspond to the ventro-tegumentaries of the anterior region of some authors.

4. The dorsal vessel is contractile and the blood in it flows from behind forwards. The dorsal vessel behind segment XIV is a great collecting vessel which receives blood from the intestinal wall and body-wall through the dorso-intestinals and the dorso-tegumentaries. Anterior to segment XIV the dorsal vessel sends out blood into branches and is therefore arterial, while posterior to segment XIII it collects the blood from its branches and therefore venous.

5. The blood from the anterior or buccal region flows through the lateral oesophageals into the oesophageal plexus, whence it flows into

the supra-oesophageal through branches proceeding to it from the oesophagus. From the supra-oesophageal vessel the blood flows into the hearts through the intestinal roots of the hearts. The lateral oesophageals on the ventral side of the oesophagus and the supra-oesophageal on the dorsal side constitute the two chief additional longitudinal venous vessels in the anterior region (segments I to XIV).

6. The ventral vessel is non-contractile and receives blood from the hearts. The flow of blood in the ventral vessel is backwards behind the hearts, and forwards in front of the hearts. Behind segment XIV the blood leaves the ventral vessel through ventro-intestinals and ventro-tegmentaries to the gut-wall and body-wall respectively, whence it is returned as stated above into the dorsal vessel. Anterior to segment XIV the blood from the ventral vessel flows forwards towards the anteriormost region, where it is distributed by the branches borne by it, and thence returned into the lateral oesophageal vessels.

7. Sub-neural and sub-intestinal vessels are absent.

8. The arrangement of the blood vessels in the region of the intestine is typical.

9. The lateral oesophageal vessels may be considered to be specialized vessels of the intestino-tegmentary system, as they are intimately connected with the intestine and the integument through their branches.

10. A pair of parietal vessels is present connected in segment XIII with the lateral oesophageal vessels, with the vessels in the integument in segments XIV to XVII, with the intestine in XV, XVI and XVII and with the prostate glands in XVIII.

They return blood from the skin and prostate glands partly directly into the intestinal plexus and partly indirectly through the lateral oesophageal vessels.

BIBLIOGRAPHY.

- Bahl, K. N., 1921.—On the Blood-vascular system of the earthworm *Pheretima* and the course of circulation in earthworms. *Quart. Journ. Micr. Sci.* LXV, pp. 350-392.
- Beddard, F. E., 1895.—*A monograph of the order Oligochaeta*, Oxford, 1895.
- Bleakly, Maurice, 1935.—The Vascular system of *Octochaetus thomasi*. *Quart. Journ. Micr. Sci.* LXXVIII.
- Bourne, A. G., 1891.—On *Megascolex coeruleus* and a theory of course of blood in earthworms. *Quart. Journ. Micr. Sci.* XXXII.
- Gates, G. E., 1938.—Indian Earthworms, IV The genus *Lampito* Kinberg. V *Nellogaster*, gen. nov., with a note on Indian species of *Woodwardiella*. *Rec. Ind. Mus.* XL, pp. 403-429.
- Johnstone, J. B. and Johnstone, S. W.,¹ 1902.—Course of blood flow in *Lumbricus*. *American Naturalist* XXXVI.
- Stephenson, J., 1930.—*The Oligochaeta*, Oxford.

¹ This reference was not available to me, and I have, therefore, consulted the summary of this paper in Maurice Bleakly's work.