On Megascolex cœruleus, Templeton, from Ceylon; together with a Theory of the Course of the Blood in Earthworms.

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With Plates VI—IX.

Index.

	PAGE
Introduction	49
Historical and systematic	50
Habitat	51
External characters	51
Body-cavity	55
Alimentary tract	57
Vascular system	59
Course of the blood	73
Nephridia	81
Nervous system	82
Generative system	82
Bibliography	84
Explanation of plates	85

Introduction.

During the summer of 1889 I visited Ceylon, with the view of determining the relation of the Earthworm Fauna of the island to that of Southern India.

I obtained an introduction from the Madras Government, and express here my great indebtedness to them, as well as to Sir E. Noël Walker, Colonial Secretary, to H. W. Green, Esq., Director of Public Instruction (Ceylon), and to T. C. Huxley, Esq., of Peradeniya, for their assistance in facilitating my work. To Mr. Huxley I am specially indebted for all my specimens of Megascolex cœruleus.

I obtained no fewer than thirty-eight[1] different species of

[1] Of these thirty-eight species I have only found seven in India, and at the present moment I know of about twenty-nine Indian species which I did not

earthworms, twenty-three of which are species of Perichætidæ, and with very few exceptions are species which I have not found in India. As a long time must certainly elapse before I shall be able to publish complete accounts of all these forms, and the general views to which their study has led me, I publish here a special account of some structural features of Megascolex cœruleus, especially the details of its circulatory system, which its great size has enabled me to work out. Where I have dealt with matters other than those relating to Megascolex I have, as a rule, embodied them in foot-notes.

Historical and Systematic.

There cannot be the slightest doubt but that the worm here described belongs to the same genus as the worm described by Beddard (1)[1] as Pleurochæta Moseleyi.

This author (2), after an examination of the type specimens of M. cœruleus in the British Museum and in Edinburgh, and subsequently to the publication of the paper above referred to, came to the conclusion that his genus Pleurochæta was identical with the genus Megascolex established in 1845 by Templeton (14). I am convinced that the species also are identical, and that the name Pleurochæta Moseleyi must be considered as cancelled. It is perfectly true that, owing to the loss of the "Memnon," by which ship Templeton despatched to England his original memoir, the existing description is very scanty; but on the one hand we have Beddard's examination of the type specimens, and on the other the worm is very large (the largest known Perichæte) and of a striking colour, and from numerous inquiries which I made on the spot is, it appears, well known to Europeans and natives, and believed to be the only worm of that size in the island.

The question of the identity of M. cœruleus with any of

find in Ceylon, making the amazing total of about sixty-seven species; and I have no reason to suppose that the field is by any means exhausted. In the town of Madras there are four species: Perichæta armata, two new species of Acanthodrilus, and a minute species of Moniligaster.

[1] These numbers refer to the bibliography at the end of this paper.

Schmarda's species is much more difficult. That Schmarda himself was led away by a mistaken interpretation of Templeton's description has often been pointed out. Templeton wrote, " Each ring is dilated in the middle of its length into a ridge, which carries on it, except in the mesial line of the back, minute conical mammillæ, two in number, each surmounted by a minute bristle;" while Schmarda (13) speaks of " the ridges which in Megascolex were stated to be found only on the dorsal side, continued in our specimens also on to the ventral side."

It is just possible that the Perichæta leucocycla of Schmarda may be the same worm ; I am unable to identify it with any other species I found in Ceylon.

As to the best use of Schmarda's generic term Perichæta I shall speak in a subsequent paper. I agree entirely with Rosa (11, A) in his classification of the Perichætidæ as far as it goes, but am convinced that it will be necessary to create several other genera.

Habitat.

All my specimens of Megascolex cœruleus came from the neighbourhood of Kandy and Peradeniya and the hills near, that is to say, from an elevation of about 1700 feet. I have no reliable information as to its occurrence at any higher or lower level. I was not fortunate enough to obtain a specimen myself, and so be enabled to note any peculiarities as to its habitat.

External Characters.

Colour and Size.—The general appearance, colour, and size may be judged from figs. 1 and 2.[1]

[1] I am indebted to my wife for coloured external views of all the worms which I have procured in a living state, and shall not give any further description. Probably no two observers would agree in describing the colour of an earthworm, and an accurate figure of a full-grown living specimen gives a better idea of the size than any measurements. In no case can we rely absolutely upon measurements of length, as the worm is constantly changing its amount

The pigment changes very slightly, at any rate for some months, when the worm is preserved in spirit; but the reddish portions shown in the figures, which are due to absence of pigment and great blood supply, naturally disappear when the specimen is placed in spirit. When the worm is alive these red portions are very noticeable, and indicate the greatly increased blood supply in the prostomium and round the mouth, and in the neighbourhood of all the genital apertures (fig. 2).

Number of Segments.—I have counted the number of the segments in specimens varying from 10 inches to 32 inches in length, and have found it to vary between 250 and 290, being usually about 270. In fig. 1, 286 segments are shown.

Prostomium.—This is, as is often the case, of a blood-red colour, and is broad and blunt at the extremity; there is a short transverse groove along its line of junction with the peristomial (buccal) segment, and both it and the latter segment present in spirit-preserved specimens numerous longitudinal grooves.[1]

Setæ.—In shape the setæ are, as compared with those of many perichæte worms, short, stout, and only slightly curved.

As to their position, they are of course arranged in rings,

of contraction, and a contraction which produces a considerable alteration in length produces a barely measurable increase of thickness.

It is interesting to note that worms of some species possess a much greater power of contraction than others. P. mirabilis, for instance, contracts and extends itself to but a very slight degree, and has a movement like a Nematoid, while Moniligaster grandis can contract itself to about a quarter of its fully extended length.

[1] We have at present few data to enable us to make much use of the prostomium in classification. It will be necessary to compare its structure in a large series of living worms. In preserved specimens it becomes contracted to a large and very variable extent. Moreover, it never has when the worm is alive the same shape for two seconds together. Many worms have a habit of constantly protruding a large portion of the pharyngeal region, and there is no line of demarcation between the prostomium on its ventral side and this latter region.

and there is a small gap in the ring in the median dorsal and ventral lines. The dorsal and ventral gaps are equal in the greater part of the body to the interspaces between three or four of the neighbouring setæ. The seta gaps are throughout smaller in the ventral than in the lateral and dorsal regions.

In the most anterior segments the gaps, especially in the lateral and dorsal regions, and above all the median dorsal gap, are much larger than in the posterior segments. The number of the setæ is greater than in any other recorded Perichæte. There are 120 to 140 in most segments, but considerably fewer in the most anterior segments. I have found as few as thirty-six in segment v.[1]

The most ventrally placed setæ, especially in the neighbourhood of the male pores, are a little larger than usual, but I should not speak of them as "modified" setæ. There are no setæ in segment XVIII between the male pores.[2]

I have never found the setæ absent from the clitellum, as

[1] I am in the habit of counting the setæ in segments v, IX, and XXV, the latter segment serving as a type for the rest of the body, and I find that the relation of these numbers to one another varies with other important characters rather than the actual numbers themselves.

The method I adopt in examining the arrangement of the setæ is to cut open the freshly killed worm on one side of the dorsal median line, to scrape out the viscera, to flatten the body-wall of the most anterior twenty-five segments between two glass slips, and to allow it to harden in spirit; subsequently to treat this piece of skin with potash followed by glycerine, and then to mount it.

This process renders it possible to see the follicles, even where the actual seta has fallen out.

The shape of the setæ varies so slightly in different species, that except in special cases it is of little use for classificatory purposes. In a preparation made as above, modified setæ in the neighbourhood of the spermathecal apertures or male genital pores should always be looked for.

[2] The presence or absence of setæ in segment XVIII between the male pores is a most important character among the Perichætidæ. In all worms which I think on other grounds it will be advisable to place in the genus Perichæta *s. str.* such setæ are present. They are also present in certain other worms which have other special peculiarities, but in a very large number of species, e.g. P. armata, and the majority of Fletcher's Australian species, they are absent.

recorded by Beddard (1), but then in none of my specimens was the clitellum very well developed.[1]

Clitellum.—The clitellum is not shown in my coloured figure, as I was unable to secure a live worm in which it was developed, but I have seen it in spirit specimens collected at some other time of year.

I have seen it developed upon the posterior portion of segment XIII, and upon every succeeding segment down to and including segment XXI; it is, however, always deficient ventrally from segment XVII onwards, so that the male pores do not actually open through clitellar substance.[2]

Genital Apertures.—The spermathecal apertures are placed between segments VII . VIII and VIII . IX, or rather just on the anterior margins (which is the usual arrangement) of the hinder of those segments in each case. They are all placed equally near the median ventral line, and about in a line with seta 9 (i. e. the ninth seta from the median ventral line).

The two oviducal apertures are placed very close together, and very slightly in front of the seta ring in segment XIV[3] (fig. 2).

[1] With regard to the presence or absence of setæ on the clitellum a good deal of unnecessary confusion exists. In all young perichæte worms which I have examined setæ are present on the clitellar segments, but when the clitellum develops they may remain projecting, or they may become buried in the clitellar substance, or any or all of them may actually drop out. I am inclined to think that all the species of one genus behave in the same way in this respect, but am not sure of this.

[2] I know of no perichæte worm in which the male pores do thus open. We shall have to distinguish between worms in which the clitellum forms a definite girdle, strictly limited in normal individuals to certain segments, and those in which it always shows a tendency to spread somewhat irregularly. Even if we abandon, as Vejdovsky (15) and Rosa (11, A) do, and as we certainly must, Perrier's classification (8) of earthworms into Anteclitellians, Intraclitellians, and Postclitellians, we may still use the character of the clitellum in classification.

[3] I know of no Perichæte in which there are any setæ between the oviducal pores; the latter always lie either in the ventral seta gap or slightly in front of the seta ring altogether. It is often a very difficult matter to ascertain whether the oviducal pores are paired or single and median.

I am now convinced that P. saletensis and P. bivaginata, which I

The male pores lie immediately ventrad of the most ventrally placed seta in segment XVIII. There are, as stated by Beddard, two other pairs of apertures in this region, though not exactly in the position stated by him. The one pair lies between segments XVII . XVIII, and the other between segments XVIII . XIX. These pores are the apertures of the glands described below (p. 83).

All these six apertures lie about equally near the median ventral line and opposite setæ 7 (figs. 2 and 13).

In the living worm there are no papillæ and no depressions in this region, but when the worm is killed and contraction of the body-wall takes place a depression is produced, as shown in fig. 13, and the pores lie at the edges of this depression, the male pores upon papillæ.[1]

Dorsal Pores.—The most anterior dorsal pore lies between segments VI and VII, and other dorsal pores occur between every two segments, including the clitellar segments.[2]

BODY-CAVITY.

This is as usual incompletely divided into separate chambers by the septa.[3]

separated chiefly because I believed them to differ in this respect, are the same species, and, indeed, the same as P. armata.

[1] There can be little doubt that the majority of papillæ which have been described in the region of the genital apertures of so many earthworms are not permanent structures, but produced by contractions of the body-wall; they are regions doubtless in which some portion of the muscular layers are absent, so that when general muscular contraction takes place they stand up as papillæ; and when a worm is so killed as to become greatly contracted these papillæ are seen, but if the same worm had been gradually killed they would not appear. Great care should consequently be exercised in using such papillæ as classificatory characters.

[2] These dorsal pores are important in classification. In some genera they are absent (Eudrilus, Teleudrilus, Thamnodrilus, Moniligaster, &c.). The position of the most anterior pore varies in different species. Sometimes they are absent from between every two clitellar segments.

[3] The body-cavity of any segment is ordinarily bounded by two septa. The anterior septum of a segment N may be conveniently termed septum N — I . N,

The most anterior septum which is well marked is septum IV . V. I have not been able to satisfy myself as to the presence or absence of any septa anterior to this. The two or three most anterior septa are usually stated to be absent, but if present they are doubtless very thin and much obscured by the muscular fibres which radiate from the pharyngeal to the body-wall. I am inclined to think, both from dissection of this big worm and from sections of smaller worms, that these septa are usually present, and that the pharynx really lies in segment I.

Septa V . VI and VI . VII are very thin.

Septum VII . VIII is also thin.

Septum VIII . IX is thicker.

Septa IX . X, X . XI, XI . XII, XII . XIII are very thick.

The three succeeding septa are less so, and the septa behind these are all very thin. From all the thick septa arise numerous muscles, some of which are shown in fig. 3. These pass backwards through one or two succeeding septa to be attached to the body-wall.

These muscles, and indeed the thickened septa, must, as has been suggested, give greater strength to the anterior end of

and the posterior one septum N . N+I. In stating that a certain organ lies in a certain segment great care is necessary with regard to two matters. In the first place, the septum may be attached to the body-wall at some spot more or less widely removed from the intersegmental groove. There is great variation in this matter in different genera; it is particularly noticeable in Moniligaster. In all such cases which I have examined by means of longitudinal sections the muscular fibres of the septum penetrate the body-wall at the right place, but have by a growth of connective tissue become adherent to the body-wall over some region behind the groove. In the second place, certain septa are at times undoubtedly absent or quite rudimentary. Perrier (9) states that two septa are absent in Urochæta. Beddard (3) also states that septum IX . X is almost absent in a species of this genus, and I have observed this to be the case in specimens of Urochæta obtained from both South India and Ceylon. The septa VIII . IX and IX . X are absent, I believe, in all the species of one genus of Perichætidæ.

The two or three most anterior septa are, moreover, absent in all worms, or so feebly developed as to have escaped notice, a fact which adds to the difficulty of enumeration.

the worm and assist it in burrowing. The conical shape of these anterior septa may be gathered from fig. 3.

Alimentary Tract.

I have little to add in this respect to Beddard's account for "Pleurochæta." I differ from him slightly with regard to the enumeration of the segments.

The arrangement of the anterior portion of the alimentary canal is shown in fig. 3.

The pharynx is bounded posteriorly by septum IV . V. This statement is not intended to exclude the possibility of there being thin, more anterior septa passing behind it. Numerous, doubtless unicellular glands lie outside on the walls of the pharynx, and open into it in the dorsal region.

The gizzard consists of an anterior thin-walled portion and a posterior thick-walled portion. Both portions are contained in the same segment. The former bears, projecting into its lumen, numerous hair-like processes which are lined by chitin and doubtless serve as a strainer. I am not aware that any such arrangement has been described in any other worm. The latter has a very thick muscular wall, and this is lined internally by thick, hard chitin. Following the gizzard is a narrow portion of the œsophagus, which extends from segment VI to IX.[1]

There is no specially large blood supply in the walls of the portion of the canal above described.

Segments X to XV contain the calciferous glands. In each of these segments the canal is swollen out into a bulb-like form, so that there is a series of such swellings, and between them in the region of the septa there are constrictions. I call these dilated portions of the œsophagus, calciferous glands, because there may usually be found in them smaller and larger concretions of carbonate of lime.[2]

[1] I use for the present the term œsophagus for any portion of the alimentary tract which lies anteriorly to the large intestine, and is not designated by any special name—as, for instance, pharynx or gizzard.

[2] I sent a number of these concretions to Professor W. D. Halliburton, of

The inner wall is much plicated, being raised into ridges and papillæ, and is excessively vascular.

The two most posteriorly placed glands are smaller than the other four.

It is beyond the scope of the present paper to discuss the relation of these glands to those found in other worms. I will merely remark that this is a very common type of calciferous gland among the Perichætidæ, though by no means the only one. It is, moreover, the simplest.

Beddard mentions no such glands in "Pleurochæta."

In segments XVI and XVII there is a further portion of the narrow œsophagus, and in the latter of these this suddenly widens out into the intestine.

The intestine is, as Beddard has pointed out, for "Pleurochæta" very complicated.

The anterior portion may be called the typhlosolar region, and the posterior the post-typhlosolar region.

The typhlosole is in a very rudimentary condition. It is a mere ridge of the intestine projecting into the lumen along the median dorsal line. As stated below (pp. 61 and 70), there is no continuous longitudinal blood-vessel running along it, but the capillary network becomes so exceedingly dense here as to form a longitudinally placed blood lacuna.

This typhlosole extends as far back as segment CXXXV.

In the anterior portion of the typhlosolar region I find the intestinal wall forming the pouches described by Beddard (1, p. 492). In segments XVII to XXXV there are the large simple pouches, and in segments XXXVI to XLII are the seven pairs of sacculated pouches which correspond very closely to Beddard's description.

Posteriorly to these sacculated pouches the intestinal wall is not protruded to any great extent into pouches.

the Physiological Laboratory, University College, London, and am indebted to him for the information that they undoubtedly consist almost entirely of carbonate of lime. But he says, "A few shreds of organic matter remain undissolved. When the concretions are treated with acid, these prove to be of proteid nature."

In the post-typhlosolar region the intestinal wall becomes much thicker. In the hinder portion of the typhlosolar region lie the remarkable "kidney-shaped glands." I find twenty-two pairs of these glands, a pair in each segment from CXII to CXXXIII. Beddard describes only fifteen pairs, lying in segments LXXXVI to CI ("or thereabouts"). With regard to structure I can confirm in every particular Beddard's account. In my sections these glands present very much the appearance which Beddard figures, and each undoubtedly opens into the intestine. When the intestine is opened and its dorsal wall examined from the inside, the two rows of apertures are perfectly clearly seen. The glands in the middle of the series are the largest, and they get smaller and smaller at either end of the series. As I have stated elsewhere (circulatory system), the typhlosole, the anterior dorsal intestinal vessel, and the series of kidney-shaped glands all cease to exist at about the same spot.

I am unable to throw any further light upon the function of these glands.

I give no account of the histology of any portion of the alimentary tract. We still want information as to the histology of the alimentary canal in earthworms, but it should be in the form of a comparative account dealing with a series of typical genera.

Vascular System.

It will be convenient to describe firstly the blood-vessels, and secondly the probable course of the blood-flow.

The red blood differs in no way from that fluid in other worms.

The Blood-vessels.

Dorsal Vessel (figs. 5 to 11, D.V.).—The dorsal vessel extends from the anterior portion of the pharynx to the last segment of the body. It lies above the alimentary canal, but is not adherent to the wall of the latter in any portion of its course. Its walls are muscular throughout its length, but most so in segments VII to XIII, in which segments the vessel is much dilated. In the intersegmental (i. e. septal) regions, where the vessel is narrowest, there are in this portion of the vessel, and in all the portion posterior to it, valves which can doubtless entirely, or almost entirely, shut off the lumen of the vessel in each segment from that in the other segments. These valves are thick, semicircular ridges of connective tissue attached to the wall of the vessel across its ventral half, and presenting an irregular free edge (fig. 12).

I have never seen the dorsal vessel double in any portion of its course. I am surprised at this, as Beddard (1) distinctly states that in his Pleurochæta Moseleyi "it bifurcates no less than five times in the first eight segments, the bifurcations always coalescing again directly."[1]

Anteriorly the dorsal vessel bifurcates—that is to say, it gives off a pair of branches which behave in a manner similar to the other dorso-tegumentary vessels (see p. 71), and are to be considered as the most anterior pair of such vessels (fig. 8).

Posteriorly the dorsal vessel ends abruptly, as shown in fig. 11.

Ventral Vessel (figs. 4, 6 to 11, v.v.).—This is also known as the subintestinal or supra-neural vessel. Its walls chiefly consist of connective tissue, doubtless élastic, with circularly disposed bands of muscle in the regions of the septa. These bands would serve to secure a specially great blood-flow in the branches of the ventral vessel in any particular region of the body. It is of very uniform calibre throughout its entire length. At its anterior and posterior extremities it

[1] To prevent any confusion upon this point I may note that I am well acquainted with the "double" condition of the dorsal vessel which has now been several times recorded; it obtains in a perichæte worm which attains nearly the same size as Megascolex cœruleus, and which I discovered on the 24th May, 1887, on the Nilgiri Hills in South India. In this worm the dorsal vessel bifurcates in each segment from VII to XVI. I have noticed a sort of longitudinal folding in of the dorsal wall in certain segments of M. cœruleus, but the vessel is not double.

terminates by bifurcating, and thus giving off its most anterior and posterior branches, which are described under the heading Ventro-tegumentary Vessels (see p. 72).

Supra-intestinal Vessels (figs. 4 to 6).—There are, as Beddard states, two of these vessels lying side by side, but widely separated, on the wall of the œsophagus in segments IX to XIII. The two are joined by commissural vessels in segments X to XIII. In segment IX they lose themselves in the intestinal capillary network, and in segment XIV they join, and a very small median supra-intestinal vessel runs on into segment XVI, where it bifurcates and joins the dorso-intestinal vessels of that segment (fig. 5). It is not continued into the region of the intestine properly so called; there is consequently no typhlosolar trunk.[1]

The supra-intestinal vessels are, as usual, closely adherent to the intestinal (œsophageal, &c.) walls.

Subneural and Latero-neural Vessels are absent.[2]

Intestino-tegumentary Vessels (figs. 4, 6 to 10, I.T.).—This name was given by Perrier (9) to a pair of symmetrical longitudinal vessels which are connected at either end with a network of capillaries, the one network being in connection with some part of the œsophageal wall (i. e. some region in

[1] In many worms the supra-intestinal vessel is said to be prolonged backwards as the typhlosolar vessel. I should not be surprised to find that the typhlosolar vessel is much more frequently absent than is supposed, if not altogether so. Benham (4, p. 286) speaks of it as an "ill-defined vessel" in Microchæta rappi. Jaquet (6, p. 346) speaks of the circulation in the typhlosole as being "très difficile à poursuivre." Vejdovsky (15, p. 110) seems a little doubtful about it, and I have frequently seen in sections blood in that region which I should have said at once lay in the typhlosolar vessel, when further examination of the series of sections has convinced me that there was only a special development of the internal intestinal capillary network, a remnant doubtless of the sinus around the intestine of many Chætopoda.

[2] Lankester (7) calls the subneural vessel the ventral vessel, but I prefer to use this latter term for the subintestinal vessel, the latter being constant in the Oligochæta, while the subneural vessel is absent in all the simpler and many of the more complicated forms, e.g. many, if not all, Perichætidæ, Pontodrilus, and Microchæta.

front of the large intestine); the other network (set of networks it really is) being in connection with the pharyngeal wall, the septa, and the body-wall. Benham speaks of them as the "lateral longitudinal" vessels. I shall show that they are only the much-enlarged representatives in the anterior region of the body of a series of similar vessels which occur, a pair in every segment, in all the remaining portion of the body. There is, in fact, in Megascolex, and I expect in many other earthworms, a vessel on each side in every segment—in all except certain anteriorly placed modified segments—a vessel which communicates with capillaries at either extremity, the one network of capillaries being in connection with the intestinal wall, and the other with the body-wall, and the blood in circulating either passes from the intestinal capillaries laden with nutriment to the cutaneous and other capillaries for the nourishment of the tissues and for its own aëration, or is collected in an aërated condition from the cutaneous capillaries to pass to the intestinal capillaries for the absorption of nutritive matters.

A discussion as to which of these two courses it takes follows the description of the vessels. There is only a single pair of such vessels in the anterior modified region, and it is this pair of vessels which has been called intestino-tegumentary vessels by Perrier. I propose to apply the term intestino-tegumentary to the whole series, and to call anterior intestino-tegumentary vessels the large anteriorly placed modified pair, and intestino-tegumentary vessels of such and such a segment those in the posterior region.

The anterior intestino-tegumentary vessels have relations with the twenty or so most anterior segments, and are, I believe, in connection with the intestino-tegumentary vessels of the following segment, and these again with those that follow, and so on, by means of capillaries or very minute vessels. The relations of the large anterior pair have been dealt with by Perrier, Horst (5), Benham, Beddard, Jaquet, and others.[1]

[1] These vessels, or at any rate some vessels having somewhat similar relations, have been stated to communicate directly with the dorsal vessel in

I merely describe here what occurs in Megascolex, without any further detailed discussion of their views.[1] The main trunks of the anterior pair of intestino-tegumentary vessels run from the sides of the pharynx, lie freely in the body-cavity in the region of the gizzard, and then gradually take up a more ventral position, passing to the inside of the hearts, without being connected with them, till they become adherent to the ventral wall of the œsophageal (calciferous) glands.[2] The anterior extremity of each is connected with a network of capillaries on the pharyngeal wall. This network is connected with the network into which the most anterior branches of the dorsal and ventral vessels break up in this region (fig. 8). Passing backwards they are joined by various branches in the regions of the septa. An inspection of figs. 4 and 8 will show that these branches are segmentally arranged, and are connected with capillary networks on the septa and in the body-wall, which communicate on the one hand with either the ventro-tegumentary vessels or with branches of the most anterior heart, and so also with the ventral vessel. One specially large branch, which has also connections with the hearts of segments VI, VII, and VIII, communicates with a special network on the gizzard; another with the networks which are also connected with the four most anterior pairs of ventro-tegumentary vessels, and so on (see fig. 4). In segments X to XIII, i. e. those segments in which occur the four large œsophageal glands, the arrangement is somewhat different, and is almost exactly repeated in each of these segments. One branch is connected with the peripheral capillary networks, and two or three branches are connected with the

Lumbricus. In the absence of specimens of that genus I am unable to discuss this fact, nor its bearing upon my theory as to the course of the blood.

[1] It will be seen how little my account differs from that of Perrier, whose memoirs on Urochæta and Pontodrilus are most masterly pieces of work, and to whom I here express my many obligations.

[2] In fig. 4 this vessel is shown as lying at some distance below these glands. The drawing is diagrammatic to better elucidate the relations of the branches of this vessel.

"intestinal" networks, i. e. with those networks in the walls of the œsophageal glands.

The other intestino-tegumentary vessels have relations which are precisely similar to one another (figs. 4, 7, 9, 10). The main portion of the vessel in each case lies closely adherent to the body-wall just behind a septum, i. e. in the anterior portion of a segment; the ventral end of it is connected by several small branches (fig. 7) with the external intestinal capillary network, while from the trunk numerous branches, especially near the dorsal region, pass to the peripheral networks. The branches of the intestino-tegumentary vessels are thus of two kinds, peripheral branches and intestinal branches. All the intestino-tegumentary vessels place the peripheral and intestinal capillary networks in communication with one another, a relationship discovered by Perrier for the large anterior pair, which led him to give them the name of intestino-tegumentary vessels, and to compare them to portal vessels. The relationship, or existence even, of the posterior intestino-tegumentary vessels does not appear to have been hitherto described. They are connected with one another, the pair of one segment with that of the adjoining segments, and the one of one side with that of the other, in the intestinal wall, and, I believe, also in the body-wall (figs. 7 and 10). The longitudinal connections in the intestinal wall constitute doubtless the infra-intestinal vessel which is figured by Howes in the 'Atlas of Biology' (Lumbricus), and is stated by Benham (4, p. 253) to have been observed by Beddard in Acanthodrilus.

Hearts.[1]—There are eight pairs of rhythmically contractile

[1] I use this term for all rhythmically contractile, circularly disposed vessels, thus including, for reasons stated below, certain anterior branches of the dorsal vessel which do not join the ventral vessel.

These hearts are either—(1) all connected with the dorsal vessel, or (2) some only are so connected, while others are connected with the supra-intestinal vessel only, or (3) some are connected with the dorsal vessel only, and some with both the dorsal and supra-intestinal vessels (in Pontodrilus and Titanus [see Perrier, **10**], in Megascolides [see Spencer, **13**], in Megascolex, suggested as a possible arrangement by Beddard and figured in this branches of the dorsal vessel; none of the other branches of the dorsal vessel, either those anterior or those posterior to these eight, are contractile.

The three anterior pairs lying in segments VI, VII, and VIII are lateral hearts; while the five posterior pairs lying in segments IX to XIII are latero-intestinal hearts, i.e. they are connected equally with the dorsal and the supra-intestinal vessels of their respective sides. An examination of fig. 5 will show that the dorso-intestinal vessels of segments XIV to XVI have similar connections, but they do not appear to be rhythmically contractile, nor have they the peculiar sphincter muscle at their distal extremities that the hearts have.[1]

The hearts of segment VI arise immediately in front of septum VI . VII (each pair of hearts arises immediately in front of the septum which divides the segment in which they lie from the segment next following). They extend only for a short distance on the wall of the gizzard, and terminate in a muscular bulb (figs. 4 and 6, *f*), a sphincter which is shut during the diastole, and opens at the systole of the heart. This heart is not connected with the ventral vessel. Two branches arise at its extremity, just beyond the muscular bulb. No branches arise directly from any of the hearts, i.e. between the point of connection with the dorsal vessel or dorsal and supra-intestinal vessels, as the case may be, and these muscular bulbs. The two branches above mentioned break up into capillaries on the walls of the gizzard, the network being connected, on the other hand, with branches of the anterior

memoir, and observed by myself in many other Perichætidæ). In all recorded cases in which there are some hearts which do not communicate alone with the dorsal vessel, such hearts are the posterior ones of the series.

I adopt Perrier's term lateral hearts for those which communicate with the dorsal vessel only, and his term intestinal hearts for those which communicate with the supra-intestinal vessel only, and shall use the term latero-intestinal hearts for those which have the dual connection to indicate tha they correspond to both lateral and intestinal hearts.

[1] These peculiar relationships show how useless it is for classificatory purposes to record simply the number of pairs of "hearts," as is often done, without detailed account of what vessels are so named.

intestino-tegumentary vessels. The hinder branch comes into relation in this way with that branch of the anterior intestino-tegumentary vessel which lies on septum VI . VII.

The hearts of segment VII are of nearly twice the length of those of segment VI. They also give off two branches from the extremity beyond the muscular bulb; the one branch has relations similar to those described above with the branch of the intestino-tegumentary vessel which lies in septum VII . VIII, and the other joins the similar branch from the heart of segment VIII and goes to the gizzard, where it, like the corresponding branch of the heart of segment VI, is in communication by means of a capillary network with the intestino-tegumentary vessel.

The hearts of segment VIII are directly connected with the ventral vessel, but between the muscular bulb and this point of connection give off two branches, one of which is mentioned above, and the other has corresponding relations with the branch of the intestino-tegumentary vessel which lies on septum VIII . IX.

The five succeeding pairs of hearts are all latero-intestinal. Those of segment IX join the ventral vessel; but, as in the case of the hearts of the preceding segment, there is a certain length of vessel between the end of the heart, as marked by the muscular bulb and the ventral vessel; from this portion arises one branch only, which has the usual relations with a branch of the intestino-tegumentary vessel—that which lies on septum IX . X. There is no branch to the gizzard-wall; we are now behind that region. All these arrangements are shown in fig. 4.

All the segmentally arranged capillary networks with which the hearts and intestino-tegumentary vessels communicate, as described above, extend over the body-wall in their own neighbourhood.

The hearts of segments X—XIII have relations precisely similar to one another. Each is connected at its proximal extremity by a vessel much narrower than itself with the dorsal vessel, and by another narrow vessel with the supra-intestinal vessel of its own side (figs. 4—6). These four pairs of hearts are much larger than any of the other hearts; they are monilated, and the muscular bulbs at their distal extremities are placed at the junction with the ventral vessel in each case; there are consequently no branches, for, as I have stated above, no branch ever arises from a heart proper. (Note in this connection the different behaviour of the intestino-tegumentary vessels in segments x to XIII; see fig. 4.)

Capillary Networks.[1]—It will be most convenient to consider these before speaking further of the vessels which put them in connection with the above-mentioned trunks.

We can, I think, recognise two groups of capillary networks only—peripheral networks and intestinal networks. I mean that there are no such things as special commissural networks placing any of the great trunks in communication with one another. If such special networks as have been described by various authors exist, placing the big longitudinal trunks in communication with one another, they may be suitably termed commissural networks. The most important of these which has been described is the network into which the dorsal vessel breaks up at the anterior extremity of the body, and which comes into relation with a similar network arising from the ventral vessel. But in Megascolex, at any rate, I see no reason why this should not be grouped with the peripheral networks. I wish, indeed, to bring into prominence the fact that we have, in the most anterior region of the body, only a series of segmentally arranged networks—nothing, in short, which differs from what obtains in other segments of the body. It must, however, be borne in mind that my investigations have been made upon a worm devoid of subneural and latero-neural vessels, the presence of which may entail other variations.

The networks which connect the dorsal vessel with the sub-

[1] Perrier (**9**, p. 466, foot-note) very justly points out that the term "capillary" is here used in a special sense, as there is nothing like the difference between a so-called capillary and a small vessel that obtains in a vertebrate animal; but the same remark applies with equal force to the use of the term in all animals other than vertebrates.

neural, described by Perrier (9) as occurring in segments VIII, X, and XIII, in Urochæta, may be special commissural networks.

Another capillary network, which, if it exists in any worm, would be a commissural network, is that connecting the dorsal and ventral vessels at their posterior extremities. From observations which I have made upon Megascolex, as well as upon some small worms, mounted alive in a compressorium, I believe that there is no such special network, but that the terminal branches of these vessels behave just like any other of their branches (fig. 11). Jaquet (6), however, speaking of Lumbricus, says that the dorsal and ventral vessels "se mettent en relation par des anastomoses réciproques" at their posterior extremities.

Peripheral Networks.—I would give this name to all the capillary networks in the skin in which the blood undergoes aëration, also those in the septa—in fact, all those which do not belong to the intestinal system; and I think we are justified in grouping all these together, as they all have similar relations with the large vessels, and are all metamerically arranged.

In Megascolex, at any rate, these always establish communication between the dorsal, ventral, and intestino-tegumentary vessels. They lie for the most part in the superficial region of the body-wall, but they are also to be found in all the various tissues and viscera, excepting only the alimentary canal, and even here the exception does not extend to the pharyngeal and gizzard region. I have not had sufficient material to work out their exact arrangement in the nerve-cord, nephridia, generative organs, or walls of the large blood-vessels, in which latter they are to be found as vasa vasorum, but I am satisfied that in all these cases they have relations similar to those of the networks found in the body-wall. I believe that in all cases branches of the dorsal, ventral, and intestino-tegumentary vessels enter into connection with them. They are certainly continuous across the dorsal median line, and I believe also from segment to segment, though not of course equally dense throughout, and it is therefore possible to speak of separate networks segmentally arranged.

The most anterior (fig. 8) is connected with the two most anterior branches of the dorsal vessel, those of the ventral vessel, and also the most anterior ramifications of the anterior intestino-tegumentary vessels.

Following these there is a series of similarly arranged networks throughout the body, the only exceptions being the slight ones about to be mentioned, and these are due to the presence of the hearts. In segments VIII to XIII the connections with the ventral vessel are wanting; in segments VI to IX there are no direct connections with the dorsal vessel, their place being taken by connections with the hearts of those segments, or rather with the vessels which are the distal connections of those hearts.

In all other segments there are connections with the dorsal vessel by means of dorso-tegumentary vessels; of the exact origin of these vessels in segments X to XIII I have no note. In all the segments as far back as XIII, and probably in the next four or five segments also, there are connections with anterior intestino-tegumentary vessels; in all the succeeding segments, and perhaps in the above-mentioned four or five segments, there are connections with the intestino-tegumentary vessels of the various segments.

Intestinal Networks.—All the capillary networks in the walls of the alimentary canal, excepting in its most anterior region, where the capillaries are more superficial and belong to the peripheral networks, fall naturally into one group, and are described below in detail for Megascolex.

These networks, as I have found them in Megascolex, differ considerably from those described as occurring in other genera. I select for detailed description one of the segments XLIII to CXXXV (fig. 10).

There are two capillary networks in the alimentary canal wall—an internal deep-lying network and an external more superficial one.

The internal network (fig. 10), which corresponds to the "quadrillage" of Perrier (9, p. 491) and Jaquet (6, p. 345), is so dense a network that it may be regarded as a blood sinus interrupted at certain spots; the interspaces are in certain places even smaller than the vessels which surround them. The meshes are not so regularly rectangular as they appear to be in some other genera; they are not equally so, moreover, in all regions of the intestinal wall. Near the typhlosole and also along the intersegmental lines the longitudinal portions of the network are specially developed, and the meshes fairly rectangular; in other regions they are less regular. The network is continuous from segment to segment, and across the dorsal and ventral median lines in each segment. The vessels are largest and the interspaces smallest over the typhlosolar region. There is indeed so much blood in this region that when the intestine is opened the typhlosole strikes the eye at once as a longitudinal band of red colour, noticeable even when the whole surface appears red. I have seen the vessels so distended that the interspaces were hardly recognisable. With the slight exceptions mentioned above, there is not very much difference in calibre among the vessels composing the network. All the vessels in any particular region may be distended or the reverse, but that is all. This internal network is directly connected with the dorso-intestinal vessels.

The external network is very different. The vessels are of very various calibres. There are large vessels which divide into small branches, and these subdivide and so on; the smallest branches form a complete network. These networks are arranged segmentally, and are not continuous, as networks, that in one segment with that in another, as is the case with the internal network. The network in each segment is continuous over the ventral median line, but not over the dorsal region. At very numerous spots little branches from the external network penetrate the intestinal wall and open into the internal network. The vessels of the external network have always clearly defined but very thin walls, do not seem capable of distension, and do not form anything like so close a network as the internal one. The vessels of the external network give one the impression of an agency for distributing blood to the lacuna-like vessels of the internal network, as indeed, I believe, they are.

The external network is formed by branches of the intestino-tegumentary vessels.

In the hinder region of the intestine precisely similar arrangements obtain, but neither network is nearly so dense, and the internal network quite loses its lacunar character.

In the anterior region it is, owing to the pouches, difficult to make a flat preparation, and so to see these networks, but from what I have seen I conclude that the differences between the arrangements obtaining in this region and those above described are only slight.

Dorso-tegumentary Vessels (figs. 4 to 7, 9, D. T.).—These are branches of the dorsal vessel connecting it with the peripheral networks. In Lumbricus, according to Jaquet (6), each divides into a "branche tegumentaire" and a "branche dorso-sous-nervien," which latter is connected with the nephridial capillaries. According to Perrier (9) a similar arrangement obtains in Urochæta; while in Pontodrilus, which is devoid of a subneural vessel, the "branche dorso-sous-nervien" is suppressed; this is also the case in Megascolex.

All the branches of the dorsal vessel anterior to the hearts, and one pair of those branches in each segment posterior to them, belong to this category.

In the most anterior portion of the dorsal vessel they arise from this latter slightly irregularly, i. e. unsymmetrically (fig. 8).

In the region of the three pairs of lateral hearts and the most anterior pair of latero-intestinal hearts there are no such vessels.

In the region of the four posterior pairs of latero-intestinal hearts there are such branches, but I have no note as to their exact place of origin. It may be some months before I obtain any fresh material, and it is a point of such minor importance that I leave it undetermined.

In all other segments they arise, regularly, from the dorsal vessel immediately posteriorly to the septum which forms the anterior boundary of the segment in which they lie.

Ventro-tegumentary Vessels (figs. 4, 7 to 9, V. T.).—These are branches of the ventral vessel connecting it with the peripheral network. There is a pair of these vessels in every segment of the body except the first, in which there is a branch of that belonging to the second segment (fig. 8) on each side, and except in those segments in which the ventral vessel is joined by hearts, viz. VIII to XIII.

As mentioned above, the hearts of segments VI and VII do not join the ventral vessel, and in these segments there is, as usual, a pair of ventro-tegumentary vessels.

In the last segment of the body the ventral vessel simply comes to an end by giving off two of these branches (fig. 11).

Dorso-intestinal Vessels (figs. 4 to 7, 10, D. I.).—These are branches of the dorsal vessel placing it in connection with the intestinal capillary networks. In segments I to IX there are no such vessels. In segments X to XIII their place is taken by vessels opening into the supra-intestinal vessels, of which there are two pairs in each segment. These may be called supra-intestino-intestinal vessels. In segments XIV to XVI there is a single pair in each segment, connected, as are the latero-intestinal hearts, with both the dorsal and supra-intestinal vessel (see fig. 5). In segments XVII to CXXXV there are two pairs in each segment, the anterior one being always smaller than the posterior (fig. 10). In segment CXXXVI and the following segments to the end of the worm there is only a single pair in each segment, the pair which corresponds to the posterior pair of segments possessing two pairs.

These dorso-intestinal vessels are usually covered by the yellowish-brown cœlomic epithelium cells which are so constantly found in the dorsal region of the alimentary canal.

The vessels in the segments anterior to the large intestine soon penetrate the intestinal wall; of those in the region of the large intestine, where there are two to the segment, the anterior one always passes round to the ventral region before penetrating the wall, while the posterior one, after having received a number of little branches (fig. 7), soon penetrates the intestinal wall. After penetrating the wall both vessels pass on towards the ventral line, receiving numerous branches from the internal capillary network.

All these dorso-intestinal vessels are formed by the lacunar network, the anterior pair rather nearer the ventral median line than the posterior pair (fig. 10).

I have now described all the important vessels in Megascolex.[1]

Course of the Blood.

Having described all the principal vessels and their relations with one another, I shall now discuss the probable course of the blood, and put forward a theory which is on the whole simpler than any which has been hitherto propounded.

The reader should bear in mind throughout the description that, according to my theory, so long as the modified anterior extremity, about the first twenty segments, remain intact, and the thereby injured extremities of the longitudinal vessels shrink so as to prevent bleeding, it is possible to remove any or all of the succeeding segments without interfering at all with the circulation—a most important condition of any tenable theory, and, moreover, a state of things which indicates the metamerically segmented character of the vascular system, always excepting the cephalisation in the anterior region.[2]

There appears to be entire agreement among previous observers as to two points only—the forward direction of the

[1] Other special vessels have been described in various genera. In worms possessing a subneural trunk there are of course branches connected with it. These branches connect it, I believe, directly with the dorsal vessel, and indirectly with the intestino-tegumentary vessels (see Jaquet, **6**). Where large nephridia occur the capillary network in connection with them would come under the group of peripheral networks, and communicate with branches of the ventro-tegumentary vessels on the one hand, and with branches from the subneural or (? and) intestino-tegumentary vessels on the other.

[2] I shall use the term cephalised region in the succeeding paragraphs as designating that region of the body in which the vascular apparatus is not similarly repeated in each segment.

blood-current in the dorsal vessel, and the downward direction of that in the hearts.

Of the blood which is brought forwards to the cephalised region in the dorsal vessel the greater portion goes into the hearts. Further, some or all of the blood going to some of the hearts may be derived from the supra-intestinal vessels—some in worms possessing both lateral and latero-intestinal hearts, all in worms possessing both lateral and intestinal hearts; the other and most anterior hearts receive all their blood from the dorsal vessel.

When we come to the questions—1. Whence comes the blood into the dorsal vessel? 2. Does any blood leave the dorsal vessel other than in the cephalised region?—we find great difference of opinion. There is in Megascolex, and probably in other worms, no great inflow at the posterior extremity; and when the dorsal vessel is filling, it fills simultaneously along the greater part of its length. According to Perrier (**9**, p. 504) and Benham (**4**, p. 255), blood enters the dorsal vessel from what I term the dorso-tegumentary vessels. I do not believe this to be the case. Vejdovsky (**15**, p. 115) states, though without giving any reason, that the blood flows from the intestinal capillaries into the dorsal vessel, and in this I agree with him.

The problem may be stated as follows:

A large quantity of blood leaves the dorsal vessel in the cephalised region. In some worms some of that blood may come to the dorsal vessel, in that region, from the supra-intestinal vessels, i. e. from the intestinal capillaries; but what we want to determine is, does any of it come in all worms from branches connected with the dorsal vessel in the posterior regions of the body? The vessels which are so connected seem always to be of two kinds, dorso-tegumentary vessels and dorso-intestinal vessels; and there can be, I think, no doubt that, in order to constantly replenish the dorsal vessel along its whole length, blood must come from one of these two kinds of vessels. Does it come from both kinds, or only from one? If the latter, from which? I think from the dorso-intestinal vessels only. Perrier (9, p. 504) having observed the dorso-intestinal vessels full when the dorso-tegumentary vessels were empty, and vice versâ, comes to the conclusion that these two kinds of vessels play opposite rôles, and decided on other grounds that the blood flows from the dorsal vessel to the intestinal capillaries, and towards the dorsal vessel in the dorso-tegumentary vessels. Benham (4, p. 283), following in Perrier's footsteps, brought forward the arrangement of the valves at the points of junction of these various vessels with the dorsal vessel in Microchæta in support of the theory; while Vejdovsky, as I have stated above, takes the opposite view with regard to the direction of the blood-flow in the dorso-intestinal vessels at any rate.

I can confirm Perrier's observations that the two kinds of vessels in question play opposite rôles. I have made this observation in several recently killed and opened worms of large size, and also in small worms mounted whole in a live-box; further, in a large Megascolex recently killed and opened I have emptied all these various vessels in one region by gentle pressure with the finger, and then watched them refill themselves; and, moreover, I have cut a vessel of each kind and watched to discover from which of the cut ends blood flows; and, lastly, I describe below an arrangement of valves slightly different from that described by Benham for Microchæta, and having, I believe, an exactly opposite function.

Observations made in all these various ways have convinced me that the dorso-intestinal and dorso-tegumentary vessels do play opposite rôles, but in the reverse way to that imagined by Perrier.

The blood enters the dorsal vessel in each posterior segment through dorso-intestinal vessels, and leaves it by dorso-tegumentary vessels. The single pair of dorso-tegumentary vessels are always small as compared with the dorso-intestinal vessels, and there are in many worms (e. g. Megascolex) two pairs of these latter in many segments, so that doubtless more blood enters the dorsal vessel than leaves it in each posterior segment, and the excess is passed forward to be sent out in the cephalised region. With regard to the arrangement of valves, in Megascolex (fig. 12) there are valves, as Perrier has described, in the dorsal vessel between every two segments, and there is also a valve at the junction of each dorso-intestinal vessel with the dorsal vessel. These latter valves consist of a soft-looking tissue which projects as a circular ridge into the dorsal vessel, and in the centre of this is the aperture of the vessel, and when the walls of the dorsal vessel contract the effect must be to occlude the apertures of the dorso-intestinal vessels. The dorso-tegumentary vessels present no such valves at their openings into the dorsal vessel, and are placed, moreover, in the anterior portion of each segment of the dorsal vessel just posterior to the valve lying in the dorsal vessel itself, so that the effect of a forward peristaltic contraction of the latter must be to force blood into these dorso-tegumentary vessels.

I cannot help thinking that the arrangement of valves described by Benham (4, p. 283) for Microchæta needs confirmation. His theory that such a valve as he describes at the entrance to each dorso-intestinal vessel serves to direct the blood into that vessel does not seem to me to be based upon sound hydrodynamical principles.

Two additional sets of facts—the relations of the two sets of intestinal capillaries to one another, and the relations of the intestino-tegumentary vessels—lend support to my view as to the direction of the blood in the branches of the dorsal vessel; and, moreover, as there is no doubt that in a certain region blood flows from the intestinal capillaries into the supra-intestinal vessel or vessels, and so into the dorsal vessel or into some of the hearts, the opposite view presents this anomaly, that the direction of the blood-flow in the intestinal vessels varies according to it in different regions; in other words, that some of the dorso-intestinal (or it may be supra-intestino-intestinal) vessels are efferent intestinal vessels and others afferent; according to my view they are all efferent, and further, the flow of blood always takes place from the dorsal vessel to the various peripheral networks, both in the region of the body in front of the hearts and in that behind them.

The ventral vessel has two kinds of vessels connected with it—hearts and ventro-tegumentary vessels—which communicate with peripheral capillary networks.

The theory with regard to the flow of blood in the ventral vessel universally current is that it flows backwards along its whole length. I do not believe that this is the case. By far the largest amount of (I believe the only) blood coming into the ventral vessel comes through the hearts, and enters, owing to the forcible contraction of the latter, at considerable pressure. Why should it flow backwards only? What pressure can there be in the anterior portion of the ventral vessel to resist any flow in that direction? The only pressure which would tend to have this effect would be caused by the flow of blood from the anterior branches of the dorsal vessel; and if this blood flow into the ventral vessel it is probable that there is not a sufficient quantity of it to fill also the intestino-tegumentary vessels, and that the blood in these vessels also flows forwards. There are other reasons which render this unlikely; but even supposing it were the case, we have on the one hand pressure caused by the flow of blood from the dorsal vessel, which passes through the dorso-tegumentary branches and through peripheral capillary networks, and added to this pressure caused by the flow of blood which has (according to the assumption) passed through intestinal capillaries, through the intestino-tegumentary trunks, and finally through peripheral networks; while on the other hand we have pressure caused by the simultaneous contraction of all the largest and most powerful hearts. There can be no doubt which of these two pressures would be the greater—the latter. I conclude, therefore, that with regard to the ventral vessel, all the blood which enters it comes from the hearts, and that all the ventro-tegumentary branches—those anterior to the hearts, as well as those posterior to them—are efferent vessels. So far as the ventral vessel itself is concerned, they carry blood away from it.

We must now consider the intestino-tegumentary vessels, and we shall find that the conclusion we have just arrived at simplifies matters enormously with regard to these vessels. There has hitherto existed considerable uncertainty as to the direction taken by the blood in these vessels. Perrier (**9**, pp. 496, &c.), after an admirable discussion of the subject, in which he was evidently tempted, on account of the connection between the capillaries at the anterior extremities of the only pair of these vessels known to him and those at the anterior extremity of the dorsal vessel, to believe that there was in the vessels in question a backward flow, a conclusion to which he afterwards came for Pontodrilus, states that the blood flows forwards in them, in Urochæta. If, as I have asserted on independent grounds, the blood flows forwards in the portion of the ventral vessel anterior to the hearts, all difficulty disappears, the blood flows from the dorso-tegumentary and ventro-tegumentary vessels into peripheral networks, and from these into the intestino-tegumentary vessels, and from these again into the intestinal capillary networks. So that the afferent vessels of these latter are the intestino-tegumentary vessels, which accords with the theory that I have advocated above that the dorso-intestinal vessels are their efferent vessels. These arrangements obtain not merely with respect to the large anterior pair of intestino-tegumentary vessels of the cephalised region, but also with respect to those which occur in every other segment of the body. Yet one more point with regard to the subject of the preceding paragraphs. According to previous theories the blood at the anterior region in such a worm as Megascolex either flows forwards in three trunks and backwards in one, or backwards in three trunks and forward in one; if what I have said is true, the blood flows forwards in two trunks and backwards in the other two, which, as all four trunks are of approximately the same calibre when filled, seems a more probable arrangement.

Further, a reference to the various memoirs will show what doubt there has always been as to any special peripharyngeal vessel, i. e. pair of commissural vessels uniting the dorsal and ventral vessels at their anterior extremities. The existence of a peripharyngeal vessel would be, of course, inimical to my theory. Even Jaquet (6, p. 340, and fig. 35), who asserts its existence, figures it as becoming capillary at one portion of its course. I am certain that it does not exist in Megascolex; in fact, the capillaries of the most anterior branches of the dorsal and ventral vessels are not connected from a functional point of view with one another, but all with those of the intestino-tegumentary vessels.

It follows from what I have said that, with regard to the capillary networks, the afferent vessels of the peripheral networks are in all cases branches of the dorsal and ventral vessels, while their efferent vessels are branches of intestino-tegumentary vessels, and the afferent branches of the intestinal networks are branches of the intestino-tegumentary trunks, and their efferent vessels are branches of either the typhlosolar, the supra-intestinal, or the dorsal vessel, so that blood coming from them is driven either into the hearts or into the dorsal vessel at its anterior extremity, and thus in either case into peripheral networks, so into the intestino-tegumentary system, and once more into the intestinal capillaries.

Every observation which I have made in Megascolex tends to bear out this theory of the circulation. The theory has, as I have implied above, this undoubted merit, that it exhibits the vascular system as a perfectly metamerically segmented organ, that portion of it contained in the cephalized region representing, as a whole, almost exactly the portion contained in any other segment of the body; the former has undergone, in fact, a synthesis, and certain additional structures, the hearts, have become developed in this region.

I may add a word or two about certain special points.

The narrow portions which join the heart to the dorsal or supra-intestinal vessels, or to both, found in so many worms, possess no little interest. In the most complicated case, that of a latero-intestinal heart, blood flows into the heart from the dorsal and from the supra-intestinal vessel, and fills it; the muscles at the point where the heart swells then act like a sphincter (they appear to have such a structure), and when the heart contracts blood cannot flow back into either vessel. Again, the muscular bulbs at the distal extremities of the hearts probably act like sphincters, and ensure distension of the hearts during their diastole, so that the systole has greater effect; and after the systole their contraction prevents regurgitation from the ventral vessel. Again, it is interesting to recall here what is stated above with regard to the intestinal capillary networks. Blood flows from the external network into the lacunar spaces, forming the internal network, and at very low pressure—a circumstance favorable, doubtless, to intestinal absorption; thence it drains away gradually into the dorsal vessel; indeed, I expect that there is some slight pumping action exerted by the latter. Moreover, the anatomical arrangements of these intestinal networks indicate in some slight degree the probable direction of the blood-flow; the external network looks like an agency for distributing the blood to the lacunæ, and in so far as this is the case it bears out what is stated above with regard to the direction of the flow.

The peripheral networks deserve a special note in respect of their triple connections. They are always supplied with blood by two vessels in which there is some pressure, and so the blood is pushed on into the third, which is always some branch of an intestino-tegumentary vessel, and which thus always conveys the blood to the intestinal wall. The arrangement of such vessels as those shown in fig. 4, *g*, passing from periphery networks in the region of the calciferous glands to the intestino-tegumentary vessels, once struck me as presenting a little difficulty. I mean that, as it must according to my theory, blood should be flowing towards the main trunk of the intestino-tegumentary vessel in them, whilst it is flowing away from it in branches which open close by them and go to the intestine. But it must be remembered that the whole question is one of relative pressure. In no part of the intestino-tegumentary system can the pressure be very great, as it is only connected with the contractile vessels by means of capillaries; but the vessels in question form part of a set of branches through which blood is entering the intestino-tegumentary system at a certain pressure, which, however slight, would be greater than that in the intestinal capillaries; into these latter the blood would consequently flow.

Summary.—The vascular system consists of a portion in the cephalized region, and of other portions metamerically repeated in all succeeding segments.

The cephalized portion differs only from that occurring in any other segment in having undergone a synthesis, and also in the presence of contractile hearts.

Throughout the body blood is forced from the contractile vessels into peripheral networks; thence it is conveyed by a system of intestino-tegumentary vessels to intestinal capillaries, and from these it returns to the contractile vessels.[1]

Nephridia.

Nephridia are present in the form of minute scattered tubules, and may be seen over almost the entire extent of the body-wall. There are no large tufts of tubules.

I have not at present worked out the structure of these Nephridia; they present peculiar difficulties in that they are most minute (actually smaller than in any Perichæte known to me), and at the same time the body-wall, as might be expected from the great size of the worm, is exceedingly thick.

[1] The theory, based upon observations on Megascolex, which I have put forward with regard to the circulation, brings us to such a plausible generalisation, and is borne out by so many structural details, that I cannot help thinking it will be found to have a very general bearing among earthworms, and it may be worth while to speculate for a moment as to the position in the scheme of the subneural vessels possessed by so many worms. So far as I can gather from the descriptions of the relations of such vessels they are in direct connection with the system of contractile vessels, and probably in indirect connection by means of peripheral networks with intestino-tegumentary vessels (see Jaquet, **6**, p. 340). In this case blood passes into them from the contractile vessels, and ultimately finds its way into intestino-tegumentary vessels and thence to the intestinal capillaries, and they do not thus affect the generalisations made above.

Nervous System.

I have nothing to add to Beddard's account of this structure. We have at present very few criteria for any useful comparison of the nervous system in different worms. It is, however, well known that there is less variation in the nervous system as it occurs in various worms than in almost any other system of organs. This fact—the constancy in structure of the nervous system in groups where most other organs vary greatly—so marked among earthworms and leeches, for instance, and so different from what occurs in planarians and nemertines, will doubtless acquire great interest when we know more as to the causes of variation in these lower groups of animals.

Generative System.

It would be going altogether beyond the scope of this paper to discuss in any detail the relation of this system as it occurs in Megascolex to that of other earthworms. I give a brief account only of the arrangements obtaining in Megascolex.

As the only points in which the structures in question differ greatly from those described by Beddard in "Pleurochæta" are such as anyone acquainted with the additions which have been made to our knowledge of this system of organs since the publication of Beddard's paper would have predicted, I shall not compare my account with Beddard's in detail.

Testes.—The testes (fig. 3) occur in segments x and xi, and are attached to the septa bounding these segments anteriorly, as is usually the case.

Seminal Funnels.—The seminal funnels lie of course in the same segments, and are attached to the septa bounding these segments posteriorly.

Vasa Deferentia.—The vasa deferentia, which are of course connected with the funnels, are exceedingly minute. The two on each side soon join together, and, running backwards, embedded in the longitudinal muscular layer, open into the muscular duct of the prostatic gland on each side, close to where this latter opens to the exterior. They are ciliated internally.

Prostates.—The prostates are small relatively to the size of the worm and very compact, and each is provided with a very short muscular duct.

Seminal Reservoirs.—There is a single pair of seminal reservoirs (fig. 3) which lie in segment XII. It is very unusual to find a single pair only among the Perichætidæ.

Ovaries.—The ovaries lie as usual in segment XIII, attached to the anterior septum bounding that segment. They are very large.

Oviducts.—The oviducts are very small, and open internally in segment XIII near the nerve-cord; they then pass through septum XIII . XIV and penetrate the body-wall, and open to the exterior by the pores described above in segment XIV.

Spermathecæ.—There are two pairs of spermathecæ which are of the same size and shape. They are pear-shaped, and lie in segments VIII and IX.[1] Each possesses a small cæcum, which might entirely escape observation in a dissection, as it is completely embedded in the wall of the spermatheca itself at its basal region. It is very obvious in sections, and contains spermatozoa, while the spermatheca itself is empty in my specimen. The existence of these cæcal diverticula bears out the views recently expressed by Beddard on this subject.

Accessory Glands.—There only remain to be mentioned the two pairs of small glands which open between segments XVII and XVIII and XVIII and XIX.

These I have ascertained to be small solid glands composed of clear-looking cells which are not stained by borax-carmine.

[1] There has occasionally been some confusion as to the segment in which the spermathecæ lie. They usually open in the groove between two segments and belong to the posterior of these two segments, but the septum is deficient just here, and they may occasionally be found pushed forward into the anterior of the two segments; but whenever I have found such to be the case I have pulled them back through the aperture in the septum, and it has become evident that they really belong to the more posterior segment.

These glands do not lie in the body-cavity, but are embedded in the muscular wall of the body in the spots where they severally open to the exterior. No trace of them can therefore, as Beddard says, be seen in an ordinary dissection of the worm. I cannot say what their function may be.

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EXPLANATION OF PLATES VI—IX,

Illustrating Professor A. G. Bourne's Memoir "On Megascolex cœruleus, Templeton, from Ceylon; together with a Theory of the Course of the Blood in Earthworms."

Reference Letters to Blood-vessels.

D. V. Dorsal vessel. *V. V.* Ventral vessel. *I. T.* Intestino-tegumentary vessels. *D. T.* Dorso-tegumentary vessels. *D. I.* Dorso-intestinal vessels. *V. T.* Ventro-tegumentary vessels. *H.* Hearts. *per. cap.* Peripheral capillary networks. *int. cap.* Intestinal capillary networks. *S. I.* Supra-intestinal vessels. *S. I. I.* Supra-intestino-intestinal vessels. *a.* Vessels passing from a supra-intestinal vessel to a heart. *b.* Vessels passing from the dorsal vessel to a heart. *c.* Commissural vessels joining the two supra-intestinal vessels. *d.* Anterior extremities of the supra-intestinal vessels. *e.* Posterior extremity of the supra-intestinal vessels. *f.* Muscular bulbs at the distal extremities of the hearts. *g.* Branches joining intestino-tegumentary vessel, with periphery capillary networks. *h.* Vessels from the intestinal capillary networks joining dorso-intestinal vessels. *j.* Branches joining intestino-tegumentary vessels, with intestinal capillary networks. *k.* Vessel in the intestinal wall (infra-intestinal), passing from the intestino-tegumentary system of one segment to that of another. *l.* Origin of dorso-intestinal vessels from intestinal capillary networks.

PLATE VI.

FIG. 1.—The entire worm drawn from life by Mrs. A. G. Bourne. Natural size.

FIG. 2.—Ventral view of the twenty-three most anterior segments. *m.* Mouth. *sp.*[1] and *sp.*[2] Spermathecopores (VII . VIII and VIII . IX). *ov.* Oviducal pores. ♂. Male pores. *gl.*[1] and *gl.*[2] Apertures of accessory glands.

PLATE VII.

FIG. 3.—The anterior portion of the worm dissected from the dorsal surface. The alimentary tract is represented in horizontal longitudinal section The septa have been cut in such a way as to render visible as much of the organisation as possible. Some of the generative organs are shown on the one side, and some on the other. The segments are numbered I—XIX. *m* Mouth. *ph.* Pharynx. *giz.*[1] Anterior portion of the gizzard, with straining

hairs. *giz.* Posterior portion of the gizzard, showing the thick muscular and chitinous walls. *ca. gl.*[1] The most anterior calciferous gland. *ca. gl.*[6] The most posterior calciferous gland. *int.* Intestine. *m. rad.* Radiating muscle. *t.*[1] and *t.*[2] The anterior and posterior testes of the left side. These have been completely pulled away from the septal wall to render them visible. *fun.*[1] and *fun.*[2] The seminal funnels corresponding to the two testes drawn. *sem. res.* Seminal reservoir. *ov.* Ovary. *pr.* prostate.

PLATE VIII.

FIG. 4.—Slightly diagrammatic side view of the blood-vessels of the anterior portion of the body. The intestino-tegumentary vessels and their branches are represented by a dark colour in this and the succeeding figures in which they occur, the other vessels by lighter colour. The greater portions of the hearts in Segments X—XIII have been removed. The numbers I—XIII are placed close to the branches of the dorsal vessel belonging to those segments respectively. The lines numbered IV . V—XVIII . XIX mark fairly exactly the position of the septa at the level of the vessels drawn. Portions of the alimentary canal are marked as in fig. 3. The various peripheral networks are shown diagrammatically. *a.* Vessel passing from the supra-intestinal vessel to a heart. *b.* Vessel passing from the dorsal vessel to a heart. *f. f.* Muscular bulbs at the distal extremities of the hearts. *g. g.* Branches of the intestino-tegumentary vessels bringing blood from peripheral networks. *D. I.*[1] Anterior, and *D. I.*[2] posterior dorso-intestinal vessel of one segment.

FIG. 5.—View from the dorsal side of portions of the dorsal vessel and its connections in Segments VI—XVIII. The dorsal vessel is shown cut in several places, and the cut ends turned backwards. The hearts and dorso-tegumentary vessels are shown cut short. *a. b.* As in fig. 4. *c.* Commissural vessels joining the two supra-intestinal vessels. *d.* Anterior termination of the supra-intestinal vessels. *e.* Posterior termination of the supra-intestinal vessels.

PLATE IX.

FIG. 6.—Diagram of the vessels in a segment containing a calciferous gland. With regard to the origin of the dorso-tegumentary vessel in this region, see p. 023. *B. W.* Body-wall. *B. C.* Body-cavity. Other letters as before.

FIG. 7.—Diagram of the vessels in a segment in the typhlosolar region. The arrows denote the direction of the blood flow. *I. W.* Intestinal wall. *typh.* Typhlosole. *INT.* Intestine. *h.* Vessels from the intestinal capillaries joining the dorso-intestinal vessel. *j.* Vessels passing from the main intes-

tino-tegumentary vessel to the external intestinal capillaries. *int. cap.* Intestinal capillaries. Other letters as before.

FIG. 8.—Vessels at the anterior extremity of the body. The dorsal and ventral vessels are shown, but their branches are shown on one side or the other only. The intestino-tegumentary vessels are shown on the left side only. *cer.* Cerebral ganglia. *N.* Nerve-cord. The peripheral capillary networks belonging to the first five segments are diagrammatically shown and numbered. *per. cap.* 1—*per. cap.* 5. The branches of the dorsal vessel (dorso-tegumentary vessels) are numbered I—V. The septa are indicated by a line, and marked IV . V and V . VI.

FIG. 9.—Slightly diagrammatic view of the vessels in the body-wall, which is supposed to have been laid open by a cut a little to one side of the dorsal median line. The object of this figure is to show the relations of the peripheral networks. *j. j.* are the branches of the intestino-tegumentary vessels which pass to the intestinal wall. A comparison of this figure with figs. 7 and 10 will show the whole course and distribution of one of the posterior intestino-tegumentary vessels.

FIG. 10.—A view from the inside of a portion of the intestinal wall laid open by a lateral cut to show the intestinal capillaries. The dark coloured vessels and capillaries are connected by the branch marked *j.*, and other similar branches not shown, with the intestino-tegumentary vessel. These branches are supposed to be seen through by transparency; they really lie on the outside of the intestinal wall. Both capillary networks are in reality a little finer and denser than shown in the figure. The origin of the two pairs of dorso-intestinal vessels from the internal lacunar network is shown, and marked *l. l.* *k.* is the small vessel by means of which the intestino-tegumentary system of one segment communicates with that of another in the intestinal wall, the small cut branches shown connected with this pass to some portion of the peripheral capillary networks.

FIG. 11.—View of the posterior extremities of the dorsal and ventral vessels.

FIG. 12.—View of a portion of the dorsal vessel cut open along its median dorsal line. *Sept.* Septa. *b. b.* Valves in the septal regions; the anterior one shown entire, the posterior one partially cut away. *D. T.* Apertures of the dorso-tegumentary vessels devoid of any valves. *D. I.*[1], *D. I.*[2] Apertures of the anterior and posterior dorso-intestinal vessels surrounded by the circular valves. *B.* Transverse section through the same piece of vessel in the region of the apertures of a pair of dorso-intestinal vessels to show the valves *b'*. *W.* The wall of the vessel.

FIG. 13.—External view of the region of the male pores from a spirit-preserved specimen to show the median pit. *gl.*[1] and *gl.*[2] Apertures of the accessory glands. ♂. Male pores.

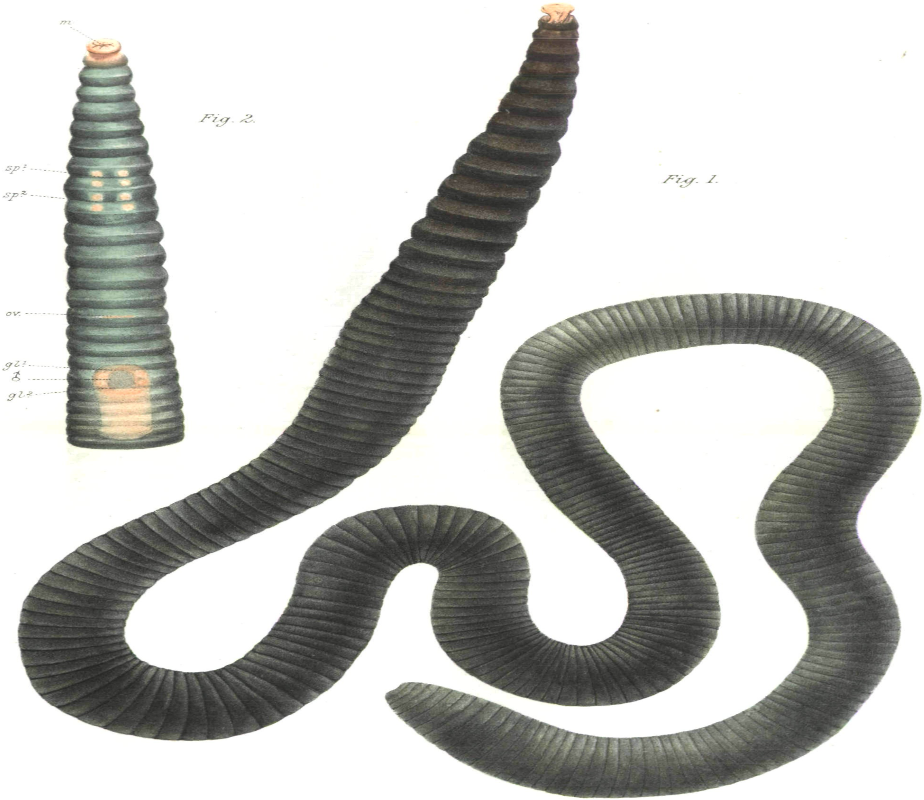

Fig. 2.

Fig. 1.

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Fig. 3.

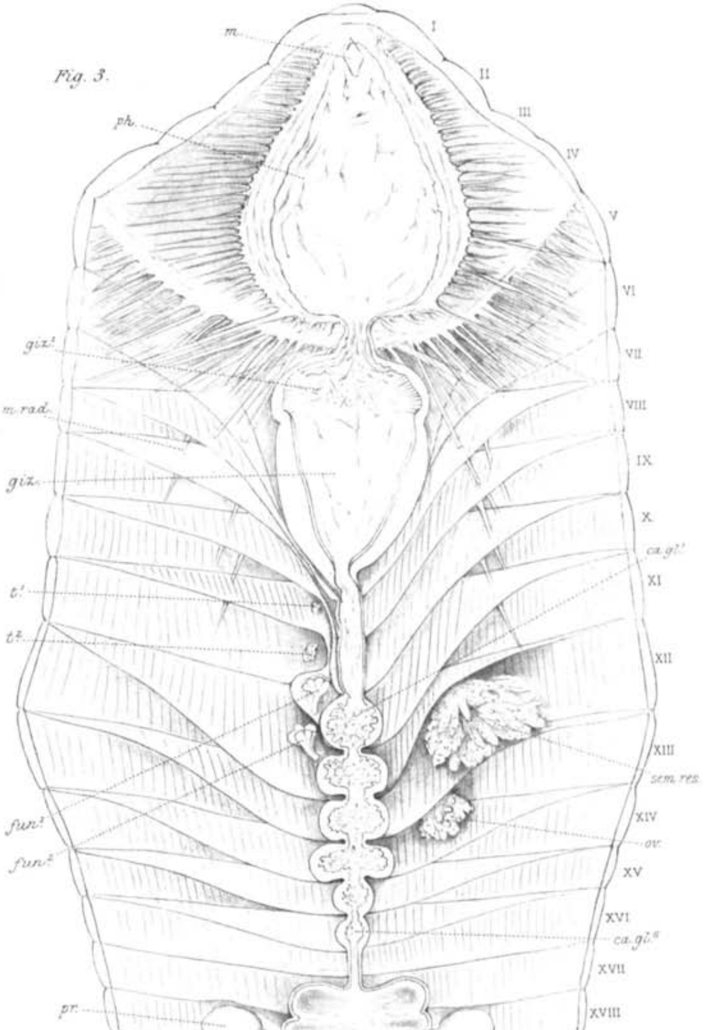

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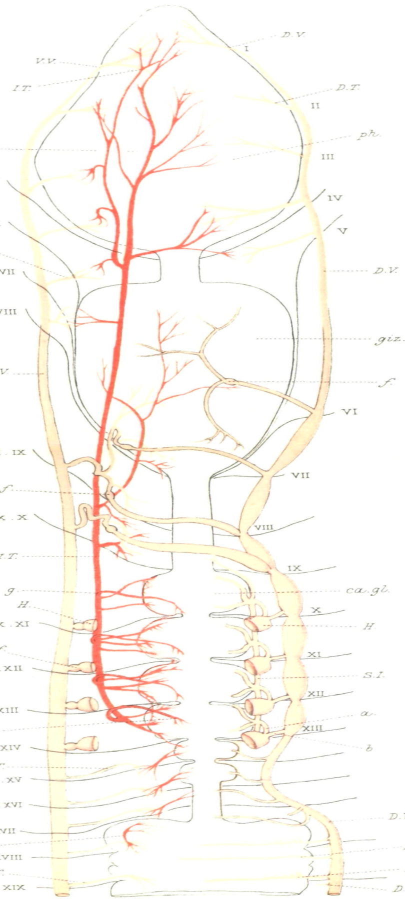
Fig. 4.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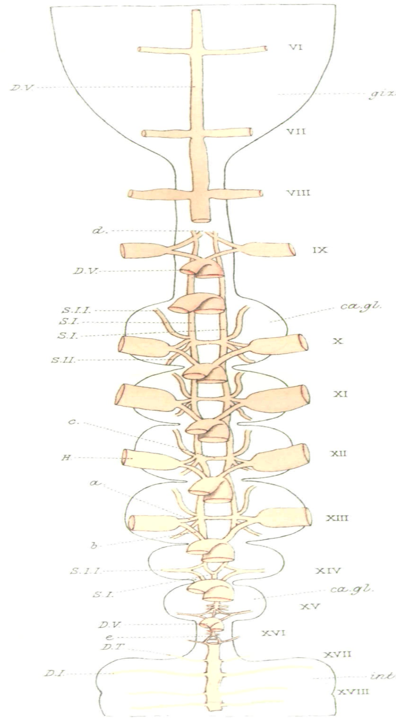
XVIII . XIX
D.T.

Fig. 5.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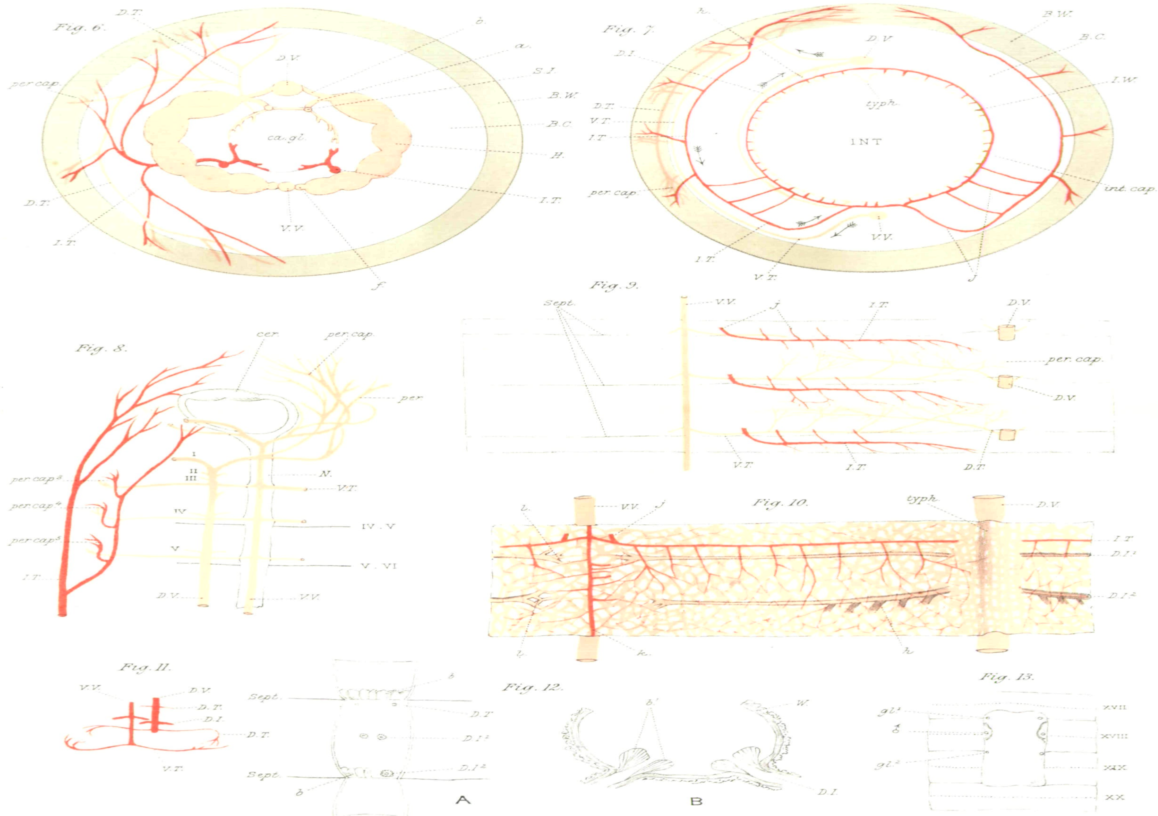

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