The Blood-system in the Serpulimorpha
(Annelida, Polychaeta)

I. The Anatomy of the Blood-system in the Serpulidae

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SUMMARY

1. An account will be given of the anatomy of the blood-system of Pomatoceros triqueter, and of comparative observations on the following serpulids: Serpula vermicularis, S. lo-biancoi, Hydroides norvegica, Vermiliopsis infundibulum, Salmacina incrustans, Protula intestinum, P. tubularia, Apomatus ampulliferus, A. similis, Spirorbis militaris, and S. corrugatus.

2. In all species there is a central blood-system of large vessels in which blood circulates in the usual manner, and a peripheral system of small blind-ending vessels which are alternately full and empty, receiving their blood from the central system, then returning it along the same channels to the central system.

3. The central blood-system is as follows: Blood moves from the tip of the abdomen to the front of the thorax through a sinus enveloping the alimentary canal. Anteriorly it passes through dorsal, transverse, and circum-oesophageal vessels to a ventral vessel in which it moves backwards to the tip of the abdomen. A pair of ring vessels connects the ventral vessel with the sinus at the posterior end of each segment.

4. The anterior end of the dorsal vessel in Pomatoceros triqueter, Serpula vermicularis, Hydroides norvegica, and Vermiliopsis infundibulum is surrounded by a sphincter muscle of unknown function, and contains a muscular valve which probably obstructs the back-flow of blood from the transverse vessel. Protula intestinum possesses the valve but lacks the sphincter. Salmacina incrustans and Spirorbis militaris have neither valve nor sphincter.

5. The peripheral blood-system has the following components: the branchial vessels with branches in the crown; the vessels of the collar and lips; the peri-oesophageal plexuses; the trans-septal vessels supplying the body-wall, parapodia, and thoracic membrane.

6. In Pomatoceros triqueter the opercular vessel is spirally coiled, but in other serpulids it is characteristically branched.

7. When Pomatoceros withdraws into its tube, movement of blood in the crown ceases. The operculum is therefore not used as a special respiratory organ when the crown is retracted.

8. The oesophagus of Pomatoceros is surrounded by two independent blind-ending vascular plexuses, an outer plexus communicating with the gut sinus and an inner plexus with the circum-oesophageal vessels. Serpula vermicularis is probably the same. Hydroides norvegica and Protula intestinum lack the outer plexus. Salmacina and Spirorbis have neither plexus.

9. The body-wall of each segment derives its blood-supply from trans-septal branches of the ring vessels of the preceding segment. In Salmacina and Spirorbis these trans-septal vessels are unbranched. In larger serpulids they have numerous [Quarterly Journal of Microscopical Science, Vol. 91, part 2, June 1950.]
branches under the epidermis, in the parapodia, and in some cases on the coelomic surface of the body-wall. Branches of the thoracic trans-septal vessels supply the thoracic membrane. In all species except *Salmacina*, *Spiroboris*, and *Protula intestinum* the thoracic trans-septal vessels end ventrally in two superficial ventro-lateral longitudinal vessels which communicate either with the circum-oesophageal vessels or with the ventral vessel. In *P. intestinum* the thoracic trans-septal vessels enter the ventral vessel directly. The pattern of superficial vessels on the ventral surface of the thorax is useful for identifying specimens.

10. Lateral vessels, such as are found in *Sabellia*, are absent in all serpulids.

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**INTRODUCTION**

This paper is the first of four which will deal with the anatomy and histology of the blood-system in the Serpulidae and Sabellidae. This research was undertaken as part of a series of investigations by Professor H. Munro Fox and workers in his laboratory on serpulids and sabellids which, together with chlorhaemids, are the only animals definitely known to possess the blood pigment chlorocruorin. The chemical and physical properties of chlorocruorin have been studied by Fox (1924, 1926, 1932, 1934, 1946) and Roche and Fox (1933), the occurrence of chlorocruorin in the Serpulimorpha by Fox (1949), and the respiration and blood circulation of sabellids by Fox (1933, 1938) and R. F. Ewer and Fox (1940). D. W. Ewer (1941) has described the anatomy of the blood-system of *Sabellia* and has made preliminary observations on its histology.

**PREVIOUS WORK**

A general account of the anatomy of a typical serpulid, *Pomatoceros triqueter*, has been published by Thomas (1940). The body consists of a prostomium bearing the branchial crown, a thorax of several segments of which the first is the peristomium, and an abdomen of many segments. The branchial crown consists of filaments which bear pinnules; one of the filaments is modified as a peduncle carrying an operculum at its tip. At the anterior end of the thorax is a collar; a thoracic membrane extends along each side of the thorax dorsal to the parapodia.

Thomas (1940) has given the most recent account of the blood-system of a serpulid, *Pomatoceros triqueter*. Earlier descriptions were published by Huxley (1855—*Salmacina dysteri*), Claparède (1868–70—*Serpula vermicularis*; 1873—serpulids in general), Haswell (1885—*Hydroides elegans* and *Pomatoceros elaphus*), Jaquet (1886—*Protula intestinum*), Meyer (1888—*Protula*.
in the Serpulimorpha (Annelida, Polychaeta)

...tubularia), Malaquin (1901—Salmacina dysteri), zur Loye (1908—Spirorbis borealis), Lee (1912—Serpula vermicularis, Hydroides norvegica, Vermiliopsis infundibulum, Pomatoceros triqueter, Salmacina dysteri, and Protula intestinum), Woskressensky (1924—Spirorbis militaris), and Faulkner (1930—Filograna implexa and Salmacina dysteri). The most important of these papers are those of Meyer, Lee, Faulkner, and Thomas. The work of Jaquet and Meyer was reviewed by Fuchs (1907), and that of Haswell by McIntosh (1918).

The main features already known of the serpulid blood-system can be summarized as follows. A sinus envelops the alimentary canal from the tip of the abdomen to the junction of the stomach and oesophagus just behind the peristomium. Here the sinus leads into a short dorsal vessel connected by circum-oesophageal vessels with a ventral vessel, which extends back along the whole length of the body and communicates with the gut sinus by segmentally arranged ring vessels. Meyer (1888) and Lee (1912) found that the first two pairs of ring vessels are branches of the circum-oesophageal vessels, the first pair leading to the dorsal vessel, and the second pair to the gut sinus; but according to all other observers the first ring vessels lead from the ventral vessel to the sinus. Meyer (1888), Lee (1912), and Thomas (1940) found a lateral vessel connecting the ring vessels on each side of the body. A peri-oesophageal vascular plexus, leading out of the sinus, was described by Claparède (1873), Haswell (1885), and Thomas (1940). Two branchial vessels leave the circum-oesophageal vessels and branch into single blind-ending vessels in each filament and pinnule. The vessels in the collar and thoracic membrane are also blind-ending. The collar vessels arise from the circum-oesophageal vessels. The vessels in the thoracic membrane are branches of ring vessels; according to Thomas (1940) the first pair of thoracic membrane vessels are branches of the circum-oesophageal vessels. Little is known about the blood-supply of the body-wall, parapodia, and intersegmental septa; branches of the ring vessels lead to these structures. According to Faulkner (1930) Filograna and Salmacina are in many ways different from other serpulids. Her work will be discussed later (p. 125).

MATERIAL AND METHODS

The following species have been used: Serpula vermicularis L., S. lo-biancoi Rioja, Hydroides norvegica (Gunnerus), Vermiliopsis infundibulum (Philippi), Pomatoceros triqueter L., Salmacina incrustans Claparède, Protula intestinum (Lamarck), P. tubularia (Montagu), Apomatus ampliferus Philippi, A. similis Marion and Bobretzky, Spirorbis corrugatus (Montagu), and S. militaris (Claparède). Pomatoceros was obtained from Plymouth, and the other species were studied at Naples. Serpula lo-biancoi, previously recorded only from the Atlantic coast of Spain, was found at Naples for the first time in 1947 by Professor H. Munro Fox, who lent me his specimens.

Observations were made on living worms, on benzidine preparations (see below), and on serially sectioned specimens. The whole of the blood-system in Salmacina and Spirorbis and the superficial vessels of the larger species can
be studied in whole living specimens. Serial sections are needed for tracing the internal vessels in species of a medium size. Most parts of the blood-system of the largest species, *Protula intestinum*, can be studied in living specimens dissected under a binocular dissecting microscope.

Like haemoglobin, chlorocruorin is a peroxidase (Lankester, 1869). In the presence of hydrogen peroxide and benzidine, a blue-black oxidation product of benzidine is deposited in the blood-vessels. This reaction has previously been used by Prenant (1921), Faulkner (1930), and Ewer (1941) for tracing the course of small vessels in polychaetes. I have employed, with equal success, the methods of Slonimsky (1927), Faulkner and Ziegler (1945). It is necessary to use thin specimens. The vessels of the body-wall of medium-sized species, such as *Pomatoceros*, are well demonstrated in preparations made by bisecting the worm longitudinally and removing the alimentary canal. Stained specimens were fixed in 70 per cent. alcohol acidified with a trace of acetic acid to control decolorization. They were then transferred to benzyl alcohol, and subsequently to Canada balsam.

The following fixatives were found to be satisfactory for serially sectioned material: 4 per cent. formaldehyde in sea-water, Duboscq-Brasil, Heidenhain’s ‘Susa’, Zenker-acetic, and Zenker-formol. Most of the sections were stained with ‘Azan’.

**Observations**

The serpulid blood-system is unusual because all the smaller vessels end blindly and are alternately empty and full of blood. They receive blood from the larger vessels, then the direction of flow is reversed and all the blood returns to the larger vessels. The movement of blood in these small vessels can be watched in the branchial crown, collar, and thoracic membrane. These blind-ending vessels constitute the **peripheral blood-system**, and the larger vessels belong to the **central blood-system**, in which the blood circulates in the usual manner. As in most invertebrate animals it flows forwards dorsally and backwards ventrally. Except at the front of the thorax, a sinus surrounding the alimentary canal takes the place of a dorsal vessel. The blood is moved forwards along the gut sinus by antiperistaltic waves of contraction of the gut muscle coat, which lies outside the sinus (Hanson, 1948a). I shall show in a later paper that all serpulid blood-vessels have muscle-fibres in their walls.

1. *Pomatoceros*

The central blood-system of *Pomatoceros* is diagrammatically represented in Text-figs. 1–4.

The gut sinus and the ventral vessel extend from the posterior end of the penultimate abdominal segment (Text-fig. 1) to the anterior end of the second thoracic segment (Text-fig. 2). In each segment the ventral vessel communicates with the ventro-lateral part of the sinus by a pair of ring vessels, which lie on the anterior face of the posterior septum of the segment (Text-figs. 3 and 4). The thoracic ring vessels are longer than those of the abdomen and are looped;
parts of them are suspended in the coelom by mesenteries attached to the septa. The chloragogen tissue of *Pomatoceros* is situated on the thoracic ring vessels and on the first few abdominal ring vessels. The gut sinus leads anteriorly into a dorsal vessel lying above the oesophagus and terminating in

**TEXT-FIG. 1.** Diagram of blood-system at posterior end of *Pomatoceros triqueter*, in ventral view.

**TEXT-FIG. 2.** Diagram to show arrangement of vessels in peristomial and second and third thoracic segments of *Pomatoceros triqueter*. Lateral view, with half body-wall removed.

da transverse vessel situated just behind the cerebral ganglia. Each end of the transverse vessel bifurcates into a branchial vessel and a circum-oesophageal vessel. The latter passes downwards through the peristomial cavity, enters the connective tissue lying under the oesophagus (Text-fig. 7), and extends backwards through this tissue to the posterior end of the peristomium, where it joins its fellow from the other side to form the ventral vessel.

The anterior part of the dorsal vessel (Text-fig. 5) is surrounded by a sphincter muscle, and contains a valve which probably ensures that blood returning from the branchial crown does not enter the dorsal vessel, but is directed through the circum-oesophageal vessels to the ventral vessel.
TEXT-FIG. 3. Diagrams to show arrangement of vessels in one thoracic segment of *Pomatoceros triqueter*, viewed from behind, (a) whole length, (b) half length of segment.

TEXT-FIG. 4. Diagrams to show arrangement of vessels in one abdominal segment of *Pomatoceros triqueter*, viewed from behind, (a) whole length, (b) half length of segment.
transverse section through the middle of this region of the dorsal vessel shows that the lumen is separated into two channels, dorsal and ventral, by a horizontal septum. Posteriorly, the septum slopes downwards and fuses with the floor of the vessel. Anteriorly, it slopes upwards and ends in a free edge where the dorsal vessel enters the transverse vessel. Clearly this septum can impede the back-flow of blood from the transverse vessel into the dorsal vessel without hindering the flow of blood in the opposite direction. The valve consists of a thin sheet of connective tissue enclosing muscle-fibres and

covered on each surface by an endothelium. The muscle-fibres enter the valve antero-laterally and pass obliquely backwards to converge towards the median line. Their contraction will presumably flatten the valve and facilitate the flow of blood out of the dorsal vessel.

The anterior end of the dorsal vessel is not visible in the living animal. The movements of the valve have therefore not been observed, nor has it been possible to discover the circumstances in which the sphincter contracts. However, the following suggestion may be made. By watching animals living in glass tubes, it has been found that movement of blood in the vessels of the crown ceases soon after it has been withdrawn into the tube; but blood continues to move forwards through the gut sinus. It is possible that the sphincter muscle contracts at this time and prevents the flow of blood into the branchial vessels from the dorsal vessel. Its contraction would divert blood through the thoracic ring vessels from the gut sinus to the ventral vessel. Unfortunately the thorax of Pomatoceros and the other serpulids which possess the sphincter

TEXT-FIG. 5. Obliquely transverse section through anterior part of dorsal vessel of Pomatoceros triqueter, to show valve and sphincter.
is too opaque for this suggestion to be tested by direct observation. The sphincter muscle was noticed by Thomas (1940). The valve has not previously been described in *Pomatoceros*, but was found by Lee (1912) in *Protula intestinum*.

The peripheral blood-system of *Pomatoceros* is diagrammatically represented in Text-figs. 2-4 and 8 and 11. The components of the peripheral blood-system are as follows: the branchial vessels and their branches in the crown; the vessels supplying the collar, lips, and anterior part of the alimentary canal; the peri-oesophageal plexuses; the trans-septal vessels with branches in the body-wall, parapodia, and thoracic membrane.

The two branchial vessels leave the central blood-system where the circumoesophageal vessels join the transverse vessel (Text-fig. 2). They enter the crown dorsally, then bend in a ventral direction; they follow the curvature of the base of each half of the crown, supply one vessel to each filament, and end in the vessels of the last filaments. *Pomatoceros* does not possess branchial vesicles, i.e. the vesicular proximal portions of the branchial vessels found in some sabellids. The filament vessels send one branch to each pinnule. The vessel of the most dorsal filament of each side gives off one branch to the adjacent 'palp'. Elsewhere (Hanson, 1949) I have suggested that the palp is a modified pinnule. The peduncle of the operculum receives a branch of the left branchial vessel. In the operculum it ends in a wide, thin-walled, blind-ending vessel, which is coiled in a spiral round a core of connective tissue and reaches nearly to the roof of the operculum (Text-fig. 6). A spiral opercular vessel has not previously been recorded in any serpulid, but the figure published by McIntosh (1926) of a longitudinal section through the operculum of *Mercierella enigmatica* suggests that a spiral vessel also exists in this species. In most serpulids the opercular vessel has branches ending in ampullae.

The good blood-supply of the serpulid operculum has naturally suggested to previous workers (Orley, 1884; zur Loye, 1908; McIntosh, 1918, 1926) that it may have a respiratory function, particularly when the crown has been
withdrawn into the tube and the operculum blocks the mouth of the tube. However, observations made on *Pomatoceros* living in glass tubes have shown that soon after the crown has been retracted the movement of blood ceases in all its vessels, including the peduncle vessel. *Sabella* behaves similarly (Fox, 1933). Therefore neither the operculum nor the rest of the crown functions as a respiratory organ when the crown is inside the tube. The movement of blood in the capillaries of the thoracic membrane and body-wall continues, and respiratory exchange is probably carried out between the blood in these vessels and the surrounding water, which is kept moving through the tube by vigorous pumping movements of the abdomen (as in *Sabella*—Nicol, 1930; Fox, 1938) and also by the activity of the ciliary tracts described by Segrove (1938) and Thomas (1940).

The two collar vessels, ventral and lateral, leave each circum-oesophageal vessel near the place where it enters the connective tissue around the oesophagus (Text-figs. 2 and 11). The lateral collar vessel supplies the capillaries on the lateral surface of the peristomium and in the lateral part of the collar. The ventral collar vessel supplies the ventral part of the collar. Soon after leaving the circum-oesophageal vessel it gives off a branch which supplies the connective tissue around the cerebral ganglia, the anterior part of the oesophagus and the buccal cavity, and ends in the capillaries of the dorsal and ventral lips.

A transverse section through the middle of the oesophagus (Text-fig. 7) shows the following layers in the oesophageal wall: the epithelium lining the lumen; a thin layer of connective tissue with a few thin-walled capillaries; a layer of circular muscles; a thicker layer of connective tissue containing numerous thin-walled capillaries; a sheath of connective tissue fibres; a layer of fatty connective tissue in which lie the circum-oesophageal vessels and several thick-walled vessels on either side of the oesophagus. These thick-walled vessels branch and anastomose with each other to form a two-dimensional plexus originating posteriorly from the gut sinus and ending blindly anteriorly (Text-fig. 2). The numerous thin-walled capillaries lying deeper in the wall of the oesophagus form a three-dimensional plexus ending blindly posteriorly and communicating anteriorly with the circum-oesophageal vessels by a small vessel on each side of the body (Text-fig. 2). There is no communication between the inner and outer peri-oesophageal plexuses. The difference in thickness of the walls of the two systems of vessels is very conspicuous. It is probable that blood-pressure is higher in the outer plexus, which is a blind-ending prolongation of the gut sinus, than it is in the inner plexus, which is supplied by one of several branches of each circum-oesophageal vessel. It may be suggested that the inner plexus constitutes the blood-supply of the oesophageal wall, whilst the outer plexus is more important as a place where blood can be received from the sinus whenever its exit from the anterior end of the dorsal vessel is prevented, for example during contraction of the sphincter muscle around the dorsal vessel.
A double peri-oesophageal plexus has not previously been described in serpulids or sabellids. Haswell (1885) noticed the outer plexus of *Pomatoceros* and found that it originated in the gut sinus; but he thought that its vessels enter the dorsal vessel anteriorly. Thomas (1940) noticed smaller inner vessels and larger, more superficial vessels in the oesophageal wall, but assumed that they constitute a single plexus communicating posteriorly with the gut sinus and ending blindly anteriorly.

![Diagram of transverse section through oesophagus of *Pomatoceros triqueterr*](image)

**Text-fig. 7.** Diagram of transverse section through oesophagus of *Pomatoceros triqueterr*.

The blood-supply of the body-wall, parapodia, and thoracic membrane is derived from trans-septal vessels, each of which has its root in a ring vessel of the preceding segment (Text-figs. 2-4 and 8). Each thoracic segment behind the peristomium is supplied by one pair of trans-septal vessels; the first pair are branches of the circum-oesophageal vessels. Each abdominal segment, except the anal segment (Text-fig. 1), is supplied by two pairs of trans-septal vessels, dorsal and ventral. All branches of the abdominal trans-septal vessels end blindly. The main branch of each thoracic trans-septal vessel, on the other hand, ends ventrally in a superficial longitudinal vessel situated in the angle between the ventral surface of the body and the flange at the ventral ends of the uncinal ridges. These two ventro-lateral thoracic vessels (Text-figs. 2, 3, and 11) originate anteriorly in the circum-oesophageal vessels and end in blind-ending branches in the ventro-posterior part of the thoracic membrane.
Branches from these vessels supply the ventral surface of the thorax, including the peristomium.

A thoracic trans-septal vessel leaves the ring vessel at the upper edge of the lateral longitudinal muscle block (Text-fig. 3). It passes through the septum and branches in the next segment. The main branch passes ventrally through the connective tissue around the muscles of the notopodial chaetae. It gives off branches to these muscles, and short, wide, blind-ending capillaries lying under the neuropodial uncini. It ends in the ventro-lateral thoracic vessel.

Soon after passing through the septum it gives off one large branch to the thoracic membrane and two or three smaller branches which end in capillaries situated just under the basement membrane of the epidermis on the dorsal surface (Text-figs. 2 and 3). Thomas (1940) has stated that the first thoracic membrane vessel is a branch of the circum-oesophageal vessel. I have found that it is a branch of the first trans-septal vessel, which originates in the circum-oesophageal vessel.

An abdominal ventral trans-septal vessel leaves the ring vessel at the lateral edge of the ventral longitudinal muscle block (Text-figs. 4 and 8), passes through the septum, and branches in the next segment into superficial capillaries in the ventral, lateral, and latero-dorsal regions of the body-wall. It also gives off short, wide, blind-ending capillaries situated under the notopodial uncini and projecting into the cavity of the segmental organ. (The segmental organ is a lateral pouch of the coelom extending dorsally into the parapodium and ventrally under the body-wall as a gonoduct, which opens to the exterior near the mid-ventral line.)

An abdominal dorsal trans-septal vessel leaves the ring vessel at the lateral
edge of the dorsal longitudinal muscle block (Text-figs. 4 and 8). There are
sometimes two, rarely three, dorsal trans-septal vessels originating in one ring
vessel. After passing into the next segment the vessel branches over the
coeleomic surface of the dorsal muscle block. Each of these branches bends at
right angles and, without branching, penetrates through the muscle block by
way of the connective tissue separating the muscle compartments, and then
emerges under the epidermis of the dorsal surface of the body. Here it gives
off a few blind-ending branches which do not anastomose with the capillaries
of the ventral trans-septal vessel. These superficial capillaries of the dorsal
trans-septal vessels are easily recognized (Text-fig. 8). They lie either parallel
to or at right angles to the longitudinal muscle-fibres, and the longitudinal
capillaries become sinuous when the muscles contract. The ventral trans-
septal vessels, on the other hand, branch at acute angles.

A few capillaries lie just underneath the epithelium of the excretory sacs of
the thoracic nephridia, but I have been unable to find their source.

Lateral vessels, such as are found in Sabella, are absent in Pomatoceros and
all the other serpulids I have examined. It is probable that Meyer (1888), Lee
(1912), and Thomas (1940) mistook trans-septal vessels for lateral vessels.

2. Other serpulids

The central blood-system of all the serpulids examined is like that of Pomat-
oceros, except for differences in the valve and muscular sphincter of the dorsal
vessel. Hydroides, Serpula vermicularis, and Vermiliopsis possess both valve
and sphincter. Protula intestinum possesses the valve but lacks the sphincter.
Spirobranchia and Salmacina lack both valve and sphincter. Suitable
serial sections of the dorsal vessels of other serpulids have not been prepared.

Whereas the central blood-system appears to be uniform throughout the
family, variations have been found in the peripheral blood-system. Some of
these variations are attributable to differences in body size, and others are at
present inexplicable from a functional point of view.

Pomatoceros is unusual in possessing a spiral opercular blood-vessel. In
other genera the vessel bears branches ending in ampullae. These vessels
have been described in Hydroides norvegica by Okada (1932–3), H. lunulifera
by Claparède (1868–70), H. uncinata and Serpula vermicularis by Orley
(1884), Apomatus similis by de St. Joseph (1894), and A. ampulliferus by
Zeleny (1905). The opercular vessel of Serpula lo-biancoi is like that of S.
vermicularis. In Vermiliopsis infundibulum the vessel branches just under the
chitinoid cap of the operculum into a number of short vessels ending in
ampullae.

Serpula vermicularis possesses a double peri-oesophageal plexus like that of
Pomatoceros, but I have been unable to discover if the inner plexus is connected
with the circum-oesophageal vessels. The outer plexus is absent in Hydroides,
Vermiliopsis, and Protula intestinum. I have been unable to trace the origin of
the small vessels found in the oesophageal wall of these serpulids. Salmacina
and Spirobranchia lack peri-oesophageal plexuses.
The blood-supply to the body-wall in Salmacina and Spirorbis is greatly reduced, presumably because of the small size of these serpulids. Salmacina is 2–3 mm. long, Spirorbis even smaller. There is a single pair of unbranched blind-ending trans-septal vessels in each segment, extending from the ring vessels of one segment to the parapodia of the next posterior segment. Ventrolateral thoracic vessels are absent.

Protula intestinum, 8–12 cm. long, is considerably larger than other serpulids. Some special features of the abdominal peripheral blood-system are probably attributable to its large size; they are not found in P. tubularia which is much smaller. The abdominal intersegmental septa, and the coelomic surface of the abdominal ventral body-wall have a rich blood-supply derived from two vessels not found in other serpulids (Text-fig. 9). Just before the ventral trans-septal vessel passes through the septum it gives off a branch which is also trans-septal, and supplies the coelomic surface of the ventral muscle block. The capillaries of the septum lie on its anterior face and lead into a small vessel which opens into the ring vessel just proximal (more towards the mid-ventral line) to the place of origin of the ventral trans-septal vessel.

Protula intestinum and Apomatus ampulliferus possess organs of unknown function on the abdominal ring vessels close to the gut sinus. They resemble the 'blood glands' of Pheretima (Stephenson, 1924). They have not been found in other serpulids. They will be described in a later paper.

Dorsal abdominal trans-septal vessels are absent not only in Salmacina and Spirorbis, but also in the larger species Serpula lo-biancoi (Text-fig. 10) and Vermiliopsis. In these two species the vessels which supply the ventral and

![Text-fig. 9. Diagram to show vessels in one half of an abdominal segment of Protula intestinum, seen from behind. Anterior septum depicted as transparent.](image-url)
lateral surfaces of the abdominal body-wall also supply the dorsal surface. *Serpula vermicularis*, unlike *S. lo-biancoi*, possesses dorsal trans-septal vessels. It also differs from *S. lo-biancoi* and from all other serpulids in that the superficial branches of the dorsal trans-septal vessels are connected with each other, on each side of the body, by a longitudinal vessel, which also receives the main dorsal branches of the ventral trans-septal vessels.

On the ventral surface of the thorax of all serpulids except *Salmacina* and *Spirorbis* there are numerous blood-vessels situated just under the epidermis and visible in living animals. This system of vessels is useful in the identification of specimens, because the pattern varies from species to species, and is invariable in its main features within any one species. Diagrams of these vessels are given in Text-figs. 11–18.

In *Pomatoceros triqueter* (Text-fig. 11) three longitudinal vessels are visible, the ventral vessel and the two ventro-lateral thoracic vessels. These three vessels are not directly connected with each other. The ventro-lateral vessels originate in the circum-oesophageal vessels and end blindly in the ventro-posterior part of the thoracic membrane. Two pairs of collar vessels, ventral and lateral, leave the circum-oesophageal vessels. In *Hydroides norvegica* (Text-fig. 12), *Serpula vermicularis*, and *S. lo-biancoi* (Text-fig. 13) each ventro-lateral vessel is directly connected with the ventral vessel by a superficial transverse vessel at the posterior end of each segment. The ventro-lateral vessels begin anteriorly in the first transverse vessel and end posteriorly in the last transverse vessel. In *H. norvegica* and *S. vermicularis* the ventro-posterior part of the thoracic membrane is supplied by two branches of the last transverse vessel. *S. lo-biancoi*, like *Vermiliopsis infundibulum* (Text-fig. 14), lacks the ventral part of the thoracic membrane. In *V. infundibulum* the
ventro-lateral vessels are situated farther away from the uncinal ridges than in other serpulids. The main collar vessel of *H. norvegica* is an anterior prolongation of the ventral vessel. *S. vermicularis* resembles *H. norvegica* except for the absence of this conspicuous collar vessel. In *S. lo-biancoi* a similar vessel supplies the surface of the peristomial segment which, in this species, is longer than usual.

*Protula* (Text-figs. 15 and 16) and *Apomatus* (Text-figs. 17 and 18) differ from other serpulids in the absence of uncinal ridges. *P. intestinum* (Text-fig. 15) is conspicuously different in that it lacks ventro-lateral thoracic vessels; the trans-septal vessels extend across the ventral surface of the thorax and enter the ventral vessel. The ventro-posterior part of the thoracic membrane is supplied by two branches of the ventral vessel. *A. ampulliferus* (Text-fig. 18) is unusual in that the first two pairs of trans-septal vessels join the circum-oesophageal vessels instead of the ventro-lateral vessels. *P. intestinum* is in many ways different from *P. tubularia*, and *P. tubularia* in many ways closely resembles *Apomatus*. Elsewhere (Hanson, 19486) I have discussed the relationship of the two genera and suggested that they need to be revised.

Faulkner (1930) has published an account of the blood-system of *Filograna implexa* and *Salmacina dysteri* in which she had described a system of sinuses which only in the anterior part of the body become restricted to form vessels. The sinus around the alimentary canal spreads into sinuses in the septa and mesenteries. These extend into sub-epidermal sinuses. The ventral mesenteric sinus takes the place of a ventral vessel. The ring vessels are wide parts of the septal sinuses, and they connect the sinuses in the dorsal and ventral mesenteries. The ring vessels sometimes have backward-pointing caeca. Anteriorly there are distinct dorsal, circum-oesophageal, and branchial vessels arranged in the usual manner. I have been unable to find mesenteric, septal, or sub-epidermal sinuses in *Salmacina incrustans*. In living specimens one can see a well-defined ventral vessel connected by discrete ring vessels with the gut sinus; each ring vessel gives off an unbranched trans-septal vessel which ends blindly near the parapodium of the next posterior segment. These observations have been confirmed in benzidine preparations and serial sections.

In benzidine preparations, Faulkner observed superficial blue-coloured patches, and in untreated animals the epidermal cells appeared to be outlined in pale green, as though blood containing chlorocruorin were present between the basal parts of the cells. From these observations she concluded that extensive sub-epidermal blood sinuses are present. I have confirmed her observations, but prefer an alternative explanation. The cell outlines are pale green in colour not only in surface view, but also in profile view; and in the latter case the outer margin of the cell also has the pale green colour. The colour therefore seems to be a property of the cell surface and is not necessarily due to the presence of a sub-epidermal blood sinus. The benzidine reaction is not specific for blood pigments, but is a reaction for all peroxidases (Prenant, 1924).
Text-fig. 11

Text-fig. 12

Text-figs. 11-12. Diagrams of ventral thoracic superficial blood-systems of: 11, Pomatoceros triqueter; 12, Hydroidea norvegica.
In benzidine preparations the vessels often have irregular outlines, and the blue-black granules are not uniformly distributed; uncoloured patches are often found. Faulkner has concluded from this appearance that the blood is not confined in well-defined vessels, but is in sinuses; for example, there is a ventral mesenteric sinus instead of a ventral vessel. However, the benzidine reaction is violent, and numerous bubbles of oxygen are liberated (see Text-fig. 6). The irregular appearance of vessels after the reaction is an artifact, although the general anatomy of the blood-system is usefully demonstrated by this method. Careful examination of living *Salmacina incrustans* leaves no doubt that its vessels have well-defined walls and are not sinuses.

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in the Serpulimorpha (Annelida, Polychaeta)