Transport of Food through the Alimentary Canals of Aquatic Annelids

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During an investigation of the blood system in polychaetes of the families Serpulidae and Sabellidae the musculature of the alimentary canal has been studied. In the following species the only muscle coat, which consists of fibres lying transverse to the main axis, lies outside the blood sinus which envelops the canal: Serpula vermicularis L., Hydrodus norvegica (Gunnerus), Vermiliopsis infundibulum (Philippi), Pomatoceros triqueter L., Protula intestinum (Lamarck), Apomatus ampulliferus Philippi, Salmacina incrustans Claparède, Spirorbis militaris (Claparède), S. corrugatus (Montagu), Potamilla sp. and Dasychone lucullana (Delle Chiaje). In Sabella spallanzani (Viviani) (Ewer, 1946) there is another layer of circular muscles between the sinus and the gut epithelium. This inner muscle coat has also been seen by Evenkamp (1931) in Laonome kroyeri and Euchone papillosa, and Dr. A. Stock (personal communication) has found it in Sabella pavonina. In the rest of the literature on serpulids and sabellids the only circular muscle coat recorded is the one situated in the outer wall of the blood sinus. It has been known for a long time (Claparède, 1873) that these muscles contract antiperistaltically, moving the blood forwards in the sinus. In the smaller species it can be seen that the antiperistaltic contraction waves not only constrict the sinus but frequently may also slightly constrict the lumen of the gut. When a contraction wave passes a food bolus the latter is moved for a short distance towards the mouth, but after the passage of the wave quickly returns to its original position. Stephenson (1913) in his well-known paper 'On Intestinal Respiration in Annelids' has shown that antiperistaltic contraction of the gut musculature is not a peculiarity of serpulids and sabellids, but, with very few exceptions, is found in all the many aquatic annelids he examined, whether or not they possess a gut sinus. Where a sinus is absent he postulated that the antiperistaltic mode of contraction of the gut musculature has been retained during evolution from ancestors possessing a sinus. Hence, in aquatic annelids in general, the contents of the alimentary canal are not moved along by peristaltic contractions of its wall as they are in other animals, but the activity of the musculature actually tends to hinder their movement towards the anus. The direction of the contraction waves in the extra muscle coat of Sabella, Laonome, and Euchone is not known.

The gut epithelium of aquatic annelids is ciliated, and it is natural to suppose that the cilia are responsible for food transport while the muscles, in
species with a sinus, have a circulatory function. However, Stephenson has stated that, with few exceptions, the cilia in the posterior part of the alimentary canal beat in a postero-anterior direction; and in some species he observed this postero-anterior beating for a long distance in front of the anus. Nevertheless, food passes down the gut and faeces leave the anus. Stephenson was especially interested in the function of this ‘ascending ciliary current’. He believed it to be respiratory. He did not demonstrate or discuss at any length how the gut contents move against the current. However, in his account of observations on the oligochaete *Aeolosoma hemprichi* he put forward an hypothesis that could be a plausible general explanation of the mechanism of food transport in all annelids with antiperistaltic muscle contraction and cilia beating towards the mouth. He suggested that the cilia move only the peripheral fluid in the gut and that this ascending peripheral current has as its complement a descending axial current, ‘since it is not to be supposed that the postero-anterior current passes through the whole length of the animal and out at the mouth’.

Recently Lindroth (1938) has made some observations which throw doubt upon the existence of an ascending ciliary current. He has pointed out that Stephenson did not demonstrate convincingly that the cilia beat towards the mouth. When one examines the abdominal gut of a small intact annelid one can see that the metachronal waves of the ciliated epithelium travel in a postero-anterior direction. To Stephenson’s list of serpulids and sabellids in which this occurs I can add: *Serpula vermicularis, S. lo biancoi* Rioja, *Hydroides norvegica, Vermiliopsis infundibulum, Apomatus ampulliferus, Salmacina incrustans, Spirorbis corrugatus, Amphiglena mediterranea* (Leydig), and *Jasmineira candela* (Grube). However, it is well known (Gray, 1928) that in many animals the direction of ciliary beat may be the opposite of the direction taken by the metachronal waves, for example, in ctenophores. As Lindroth has pointed out, Stephenson did not discriminate between the metachronal waves and the beating of the cilia. He stated only that: ‘The direction of action of the cilia is obviously . . . from behind forwards.’ Now it is very difficult to discern the direction of the effective strokes of the cilia in the alimentary canals of serpulids and sabellids: they beat too quickly. In intact specimens one cannot deduce the direction of ciliary beat from the direction of movement of particles travelling over the surface of the epithelium because, as already discussed, the contents of the gut may be moving against the current set up by the cilia. Like Stephenson and Lindroth I have noticed that small particles in the water in the vicinity of the anus may enter the rectum and travel up it for a short distance, but they are invariably expelled. Stephenson thought the entrance of particles into the rectum to be additional evidence for the existence of an ascending ciliary current; he attributed the expulsion of the particles to an inability on the part of the posterior end of the gut ‘to deal with solid particles’; ‘if possible it avoids receiving them’. Lindroth has shown that the particles are sucked into the rectum during the expansion of the rectum which follows the initiation of a wave of antiperistaltic contraction of its walls.
Lindroth has seen the direction of beating of individual cilia in the posterior part of the alimentary canal of whole small specimens of *Ammotrypane aulogaster* (Opheliidae). They were beating towards the anus. Moreover, particles near the cilia moved towards the anus, as they also did in the hesionids *Ophiodromus vittatus* and *Castalia punctata* and in an unidentified member of the same family. Lindroth did not consider the possibility that these particles might have been moving under the influence of an axial stream of water returning down the gut. His observations were all made on animals immobilized by narcotization with chloretone; although I know of no evidence that chloretone affects the beating of cilia, it would be desirable to make observations on normal animals. I have found it impossible to distinguish the direction of beating of the cilia in the intact alimentary canals of any of the serpulids and sabellids I have examined. *Salmacina incrustans*, being relatively very transparent, might be thought suitable for this purpose, but the cilia beat too quickly. Preliminary attempts to slow down their rate of movement by lowering the temperature or pH of the surrounding water were unsuccessful. Even when specimens are dying by compression and asphyxiation under a coverslip the cilia beat rapidly up to the moment when their movement entirely ceases.

In larger serpulids and sabellids one can dissect out portions of the wall of the abdominal alimentary canal and study the direction of movement of particles over the exposed ciliated surface. The interpretation of observations is then not complicated by the possibility that the particles are moving against the current set up by the cilia. In this way it has been found that in the following species the cilia beat towards the anus whilst the metachronal waves travel towards the mouth: *Serpula vermicularis, Hydroides norvegica, Vermilopsis infundibulum, Pomatoceros triqueter, Protula intestinum,* and *Sabella spallanzanii*.

Hence it is clear that the cilia in the alimentary canals of these serpulids and sabellids beat in an antero-posterior direction, and that the 'ascending ciliary current' of Stephenson does not exist. Moreover, it seems improbable that it exists in any aquatic annelids. Lindroth (1941) has already discussed the respiration of polychaetes and concluded that the rectum is not a special respiratory organ as Stephenson thought it to be.

In conclusion, it is very probable that the cilia of the alimentary canal in aquatic annelids directly aid transport of its contents. The force exerted by the cilia may be greater than that exerted by the antiperistaltically contracting muscles, but it is probable that food transport is aided by a descending stream of gut fluid initiated in the following manner at the anterior end of the gut. When the mouth is closed or when food is entering the mouth in the course of ciliary feeding, the fluid moved forwards by the antiperistaltic contraction waves is presumably forced to turn back and move down the gut towards the anus. In the same way Stephenson accounted for the transport of food in the gut of *Aeolosoma* in the face of a peripheral antero-posterior stream of water.
The metachronal waves on the ciliated epithelium of the intestine of *Salmacina incrustans* move in a postero-anterior direction, but in the wide part of the alimentary canal situated in the achaetous zone just behind the thorax the waves travel obliquely backwards, the transverse component always appearing clockwise when the animal is viewed from the anterior end. Under the influence of these cilia the bolus of mucus and food particles rotate as they move down the intestine and continue to rotate until they have left the anus. A faecal bolus is sometimes arrested half inside and half outside the anus; both parts continue to rotate. In one case a bolus in the rectum was observed rotating while all the cilia in that part of the gut were inactive. The rotation imparts a characteristic spirally sculptured shape to the bolus, and the region of greatest concentration of particles within it takes the form of a spiral. These boli invariably rotate in a direction that appears clockwise when the animal is viewed from the anterior end. This shows that the cilia causing the rotation beat in the same direction as that taken by the metachronal waves. On the contrary, as discussed above, the cilia of the intestine most probably beat in a direction opposite to that taken by the metachronal waves.

Boli rotating in a clockwise direction have also been seen in the abdominal gut of *Serpula vermicularis*, *Pomatoceros triqueuter*, and *Spirorbis corrugatus*. Spirally shaped boli have been found in the abdominal gut in *Protula intestinum*, *Sabella spallanzanii*, *Potamilla* sp., and *Dasychone lucullana*. Stephenson (1913) noticed a rotating bolus in the posterior part of the alimentary canal of a specimen of *Spirorbis borealis* and he also found rotating boli in *Aeolosoma hemprichi*, an observation that I have confirmed. Faulkner (1930) noticed occasional rotating food masses in the anterior part of the gut of *Filograna implexa*. It seems very probable that they will be found in other annelids. The rotation presumably facilitates the mixing of enzymes with the food as in *Amphioxus* (Barrington, 1937) and slows up the movement of food through the anterior part of the gut which is probably the region where enzymes are secreted (Nicol, 1930).

**Summary**

1. In most serpulids and sabellids the only muscle coat in the wall of the alimentary canal lies outside the blood sinus which envelops it. In a few sabellids there is another muscle coat, of unknown function, between the sinus and the gut epithelium.

2. The muscles outside the sinus contract antiperistaltically and tend to hinder the transport of the gut contents towards the anus.

3. The contents of the alimentary canal are transported by its cilia which beat towards the anus. The metachronal waves of the ciliated epithelium travel in a postero-anterior direction. The 'ascending ciliary current' of Stephenson (1913) does not exist.

4. The food boli of serpulids and sabellids rotate as they move down the gut. In *Salmacina incrustans* the rotation is imparted by cilia in the anterior part of the gut.
These observations were made in the Zoological Station of Naples. I wish to record my gratitude to the staff of the Station, to the British Association for the Advancement of Science for the use of its Table, and to the University of London for a grant towards travelling expenses.

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Stephenson, J., 1913. Ibid., 49, 735.