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XIV.—On Intestinal Respiration in Annelids; with Considerations on the Origin and Evolution of the Vascular System in that Group. By J. Stephenson, M.B., D.Sc. (Lond.), Major, Indian Medical Service, Professor of Biology, Government College, Lahore.

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The investigations recorded in the present paper have been carried out at various times during the last six years. A number of the observations on aquatic Oligochaeta were made some time ago in India, and, along with some of the theoretical conclusions, formed Part IV. of a Thesis ("Studies on the Aquatic Oligochaeta of the Punjab") presented in 1909 for the D.Sc. degree of the London University. This division of the paper has been considerably extended as a result of further investigations on Indian freshwater forms, and on the littoral Oligochaeta of the Clyde, the latter carried out at Millport in 1909. The portion of the present paper which is concerned with the Polychæta and smaller groups represents work done in 1909 at Millport, and in 1912, during my occupancy of the London University table, at the Plymouth Laboratory.

The observations on intestinal respiration in Oligochaeta, especially those which concern the relation of the antiperistaltic contractions of the gut to the contractions of the dorsal vessel, led me, in conjunction with my investigations into the anatomy of the circulatory system in these forms, to the views on the evolution of the vascular system which are expressed in Section 3 of Part I. My original object in studying the Polychæta was to find out whether the facts of anatomy and physiology in that group supported these views. The observations which resulted, while in a general way confirmatory, add nothing to the argument; and the consideration of the evolution of the vascular system has therefore been left at the end of the part dealing with Oligochaeta, where it most naturally occurs. Certain phylogenetic speculations, on

the other hand, which have for their basis the phenomena and the facts of distribution of intestinal respiration, come most fittingly at the conclusion of the paper.

I wish here to express my sincere thanks to Mr R. ELMHIRST, Superintendent of the Millport Marine Biological Station, and to Dr E. J. ALLEN, Director of the Plymouth Marine Laboratory, for the facilities and assistance so readily afforded me in my work at these places. My best thanks are also due to the Senate of the University of London for permission to occupy the University table at Plymouth for a month during the summer of 1912.

I. OLIGOCHÆTA.

1. THE PHENOMENA OF ANTIPERISTALSIS AND ASCENDING CILIARY ACTION IN THE INTESTINE OF AQUATIC OLIGOCHÆTA.

If one of the smaller aquatic Oligochaeta, such as a *Nais* or *Pristina*, be placed under the microscope and observed for a few minutes under a low power, the posterior part, or even in many cases the whole length of the intestine, will be seen to manifest recurring contractions, which constrict the lumen, and passing forwards in succession from the posterior towards the anterior end, die away, perhaps about the region of the stomach, perhaps some distance before reaching this point. These contractions are of the nature of those known as peristaltic; but since they always occur in a direction from behind forwards, and not from in front backwards, they may, borrowing a term from mammalian physiology, be better described as an *antiperistalsis*.

If the intestine itself be now more minutely examined—and though the phenomenon is often visible with a low power, it is at any rate more obvious with a high one—ciliary motion will probably be seen to be actively going on within the lumen of the canal. The direction of action of the cilia is obviously, like that of the antiperistaltic contractions, from behind forwards; the anus will probably be open, and if some particles of carmine be added under the coverslip, these may be seen to be swept in, and thence upwards along the alimentary canal for some distance.

These or similar phenomena have been known for some time among the Polychaeta; and it is generally recognised that, in many animals of that Order, the intestine has a respiratory function. In the Oligochaeta, the phenomena have not received much attention. Antiperistaltic movements of the intestine in Enchytræids have been described by VEJDovsky (53, p. 33), and are referred to by MICHAELSEN (32, p. 28); these authors are quoted by LANG (29, pp. 211, 212). BOUSFIELD (9) speaks of the intestine in the genus *Dero* as “having a very strong inward ciliary current for a great part of its length,” and adds, “in all the Oligochaeta a strong inward current is visible in the hinder part of the intestine, which, no doubt, subserves a respiratory purpose, as it commences at the point where the arterial system receives its blood from the venous.” HESSE (24) mentions this as a characteristic of the Naididae. Neither VEJDovsky (54) nor BEDDARD (3) refer to the phenomena in their monographs on the

Oligochaeta. The appearances are, however, very obvious, and must be familiar to all students of the group; it is surprising, therefore, that they should hitherto have received so little notice. Hence it appears useful to call attention to them, and to what they imply, viz. that the intestine in the aquatic Oligochaeta has a respiratory function.

I have already made brief mention of the occurrence of antiperistalsis and ascending ciliary action, in the anatomical descriptions of certain aquatic Oligochaeta of the Punjab (46, 47). I have since then continued and extended my previous observations, both in India and at Millport in Scotland, with results which are set forth in what follows.

NAIDIDÆ.

Nais communis Piguet, var. *punjabensis*.

The above (47, 48A), which I at first supposed to be a variety of *N. variabilis* Piguet, is one of the commonest of the aquatic Oligochaeta of Lahore; and it is one in which the antiperistaltic movements may be seen almost constantly.

Such movements usually occur fairly regularly at intervals of a few seconds. They extend forwards for a considerable distance, often as far as the stomach, i.e. to about the eighth segment. In an animal which is about to divide by fission into two, the zone of budding offers a certain resistance to the forward passage of the wave; the antiperistaltic waves, having traversed the whole length of the posterior animal, are momentarily checked at this point, and, if feeble, fail to enter the anterior animal; or, in other cases, only the more violent of the series pass forward beyond this point. Occasionally the antiperistalsis is replaced by a direct, or antero-posterior peristalsis at the hinder end of the animal; this occurred on one occasion after the animal had been under observation for some time in a small quantity of water; one may recall the fact that in the higher animals the second stage of asphyxia is characterised by violent expiratory movements.

The ascending ciliary movement is not invariably to be seen, and its presence or absence is often dependent on the opening or closure of the anus. In the same specimen the anus may at first be open and ciliary motion well marked, while later the anus is closed and ciliary motion stops. The presence of large quantities of food or faecal matter in the intestine is not a hindrance to ciliary action; this may be very well marked all along the sides of such masses, though they may almost fill the lumen.

Starina punjabensis Stephenson.

The species of the genus *Starina* are usually found coated with a layer of foreign matter, which renders the examination of their minute anatomy difficult, or in some specimens impossible. The present species (47) forms no exception to the rule, but the hinder part of the body is frequently less opaque than the anterior, and in suitable specimens it is not difficult to establish the following points:—Antiperistaltic move-

ments are always to be observed, extending usually over the greater part or the whole of the intestine. They are very regular in rhythm; the frequency may be from seventeen to thirty-six per minute. Matter in the intestine may at times be moved for some distance in an anterior direction by the antiperistalsis; or particles may be seen to oscillate, moving anteriorly for a little distance with the antiperistaltic wave, and seeming to recoil back again after it has passed, as if the pressure was now directed backwards. Faeces nearing the anus may also be carried some distance back in their course, *i.e.* anteriorly, by the combined antiperistalsis and reversed ciliary action.

A direct (antero-posterior) peristalsis was observed in this species; it was slower than the usual antiperistaltic movements, and occurred for some distance both in front of and behind the zone of budding in an animal which was preparing to divide. In one portion of their extent the movements of the gut-wall were mainly confined to the ventral side of the intestine. At the posterior limit of their extent, which was about the junction of the anterior and middle thirds of the hinder of the two components into which the animal was about to divide, they were quite overcome by the antiperistaltic movements of the hinder portion of the intestine.

The ascending ciliary action is well marked in this species, and may often be called violent; it may be very obvious with the low power. It begins at the anus, and ceases when the anus is temporarily closed. Particles of Indian ink are swept towards the anus from some little distance outside, and enter the aperture; they ascend some way up the intestine, but cannot be followed far.

Branchiodrilus hortensis (Stephenson).

In this species (48), which belongs to one of the few genera of Oligochaeta which possess gills, antiperistalsis is well marked and of general occurrence. The frequency of the waves may vary from seven to twenty-four per minute; they may be very violent, and may extend through the whole length of the intestine, reaching as far as the hinder end of the oesophagus. In some specimens the contractions were numerous, distinct, and well defined, but embracing only a small longitudinal extent of the gut-wall; the appearance was therefore that of a series of ring-like constrictions of the gut, and since these travelled slowly along, seven to nine separate constrictions could be seen in the low-power field of the microscope at once. On one such occasion their character changed while under observation; they became larger and less numerous, so that only two were in the field at the same time.

Ascending ciliary action does not always occur, the anus being frequently kept closed; it may, however, be violent and easily visible with the low power.

Aulophorus tonkinensis (Vejd.).

This species, first described by VEJDOVSKY from an incomplete specimen, has more recently been investigated by MICHAELSEN (33) and myself (49). The opportunity of

making the following observations I owe to Dr ANNANDALE, who kindly sent me living worms from Calcutta.

Antiperistaltic movements are manifested in this form also. In one case they proceeded from the anus as far forward as the tenth segment of the posterior component of a chain of two zooids, and were again obvious in the posterior portion of the anterior zooid. In another case they were observed, in the posterior component of a chain of two, only in segments x. -vii.; in the anterior component the contractions began near the hinder end, and passed forwards into the anterior half of the animal, being most violent in segments xiii., xii., and xi., and ending in segment x.; the rate was sixteen per minute.

In this last instance there appeared to be a slight check to the onward advance of the wave of contraction between segments xiv. and xiii. Later, the violent antiperistalsis previously seen in segments xiii.-xi. became less marked; and the wave of contraction often failed to pass forwards from xiv. to xiii., doing so every second or third time only.

Reversed ciliary action also occurs; sometimes, at least, it does or does not occur according to whether the anus is open or closed. In one case it reached the eleventh segment of the posterior component of a chain, in another nearly to its anterior end.

Dero spp.

It is in this genus that BOUSFIELD (*vide ante*) specially noted the occurrence of the reversed ciliary movement; it can, in fact, be easily seen with the low power. In specimens of this genus (species undetermined) found near Lahore, rapid and regular antiperistaltic movements of the intestine were also to be observed.

Both reversed ciliary movement and antiperistalsis occur also in a second species of *Dero* (described but not named by me) (48).

Other Naididae.

The phenomena of antiperistalsis and ascending ciliary action are also to be observed in *Pristina longiseta* Ehrbg.; in a *Pristina* which resembles in most respects *P. aquiseta* Bourne, though, perhaps, specifically distinct (47); and in *Stylaria lacustris* (L.).

In *Nais paraguayensis* Mehln. antiperistalsis occurs; but when I was studying this form some years ago, I unfortunately made no note as to the occurrence of ascending ciliary action or its absence, and I have not met with this species again since that time. In a specimen belonging to the genus *Naidium*, the only one that I have met with, and one which I have not specifically identified, I observed antiperistalsis of the usual kind; but no ciliary movement of any kind was seen, as the whole length of the intestine was full of food-matter.

On the other hand, I have not noticed either phenomenon in the two species of

Chaetogaster with which I am acquainted, *C. punjabensis* (45) and *C. orientalis* (described at first (46) under the name *C. pellucidus*, which, however, was preoccupied). Though cilia may be seen working in the stomach and intestine of *C. punjabensis*, their motion is by no means so obvious as in other Naididæ, and the direction is either antero-posterior or indefinite.

TUBIFICIDÆ.

Limnodrilus socialis Stephenson.

This worm was first described by me from specimens found near Lahore (51); I have since received examples from Calcutta and Ceylon.

In these animals antiperistalsis is not invariably to be seen, and at the coldest time of the year, in January, with the temperature of the laboratory about 52° F., the phenomenon was frequently absent; the worms at this period were very sluggish, and, as will be mentioned, often showed no ciliary motion in the intestine.

The antiperistaltic movements, when present, are more limited in extent than amongst the Naididæ; the most posterior portion of the gut may exhibit them, or they may be confined to a length of intestine in the middle of the body. The contractions progress slowly; thus in one case, in an animal of about sixty-five segments, where the antiperistalsis was occurring between the fortieth and twenty-first segments, each wave took about seven seconds to traverse one segment; contractions took place at the rate of eight in forty seconds, or twelve per minute; so that each segment of intestine often exhibited two distinct contractions, one in its anterior and one in its posterior part. The constrictions in all cases affect the whole circumference of the gut, *i.e.* are ring-like, and not confined to one side of the intestinal wall. The amplitude of the movements, or the actual amount of narrowing of the lumen, is not very great, but the force may be sufficient to move the fæcal masses in an anterior direction through several segments.

Ascending ciliary action is also not constant; especially it seems to fail at the coldest season of the year. It occurs, when present, in the posterior portion of the gut, and may extend for a considerable distance, or be limited to a portion of the tube immediately in front of the anus. It may be violent, and easily visible with the low power of the microscope; it may even take place during a period when the anus is closed, though, on the other hand, it may suddenly cease on the closure of the anus.

There is no necessary relation between the antiperistalsis and the ascending ciliary action; they may both occur at the same time, or either may be present without the other.

Clitellio arenarius (Müll.).

Reversed ciliary action is usually, but not invariably, to be observed in examples of this species. It may be absent in specimens in which the anus is closed; but, on

the other hand, it may be very obvious even with the low power, starting from the anus even though the anus be closed at the time. It can be followed through about the posterior ten segments of the body; after this point the body of the animal may become too opaque to allow of the phenomenon being observed further; it probably, however, extends to a considerably greater distance up the gut, since in one favourable instance it was followed up through the last twenty segments.

Antiperistalsis was noted in all the specimens observed. Its extent varies; beginning from the anus, it may be confined to a few of the most posterior segments; or it may extend for ten, thirteen, fifteen, or eighteen segments.

Branchiura sowerbyi Bedd.

I have recently had the opportunity of examining in the living condition several specimens of this interesting worm, which I found near Lahore (51).

Antiperistalsis was present in all the specimens observed; the character of the contractions, however, varied somewhat. In the first specimen the contractions, beginning at the anus, were regular, ample, and rapid; the anus opened momentarily, then closed, and the wave thereupon commenced, as if the animal were taking a gulp of water and passing it upwards along the canal. The contractions did not affect the middle region of the gut; but further forwards they were again visible, though fitful and of small extent, embracing only a segment or two of the gut here and there.

In another specimen also, contractions were frequent and ample, the lumen of the gut in the posterior part of the animal being occluded by the passage of the wave; particles were seen ascending the intestine. In one specimen it was noted that the contractions were better marked in the anterior than in the posterior part of the intestine.

Reversed ciliary action was not observed; but it may be allowable here to call attention to the intake of water by the "gulping" action of the anus. The following observation was made:—It was noted that the anus opened, and a gulp was taken; the anus closed, and the gulp was passed up the intestine by antiperistalsis; this was immediately repeated, and so on for a series of such gulps, after which the anus remained closed, and the posterior part of the intestine was quiescent for a time; then more gulps were taken at irregular intervals.

ENCHYTRÆIDÆ.

I have examined in all a fair number of species of Enchytræids; the observations were mostly made at Millport, while I was investigating the littoral Oligochaeta of the locality. All show a great uniformity, and it will not be necessary to describe each species separately.

In general, antiperistalsis proceeds continually and fairly regularly, beginning at or near the hinder end of the animal, and ending near the anterior limit of the intestine. As will be seen more fully later, this antiperistalsis serves to propel the blood in the intestinal plexus (or sinus); and its anterior limit corresponds in general to the point where the plexus or sinus passes into the dorsal vessel, which in this family exists only in the anterior part of the body; this point varies in its situation within fairly wide limits in the different genera and species.

Reversed ciliary action is in general not present.

Several observations may be cited, which illustrate the kind of phenomena occurring in this family, and at the same time show a few variations from the typical order.

Lumbricillus tuba Stephenson (50).

Antiperistalsis may begin from a point very near the posterior end of the animal, or from a point in front of this *e.g.* about nine segments from the end. In one case the contractile wave originated from a point corresponding to the septum between the eleventh and twelfth segments, reckoning from the hinder end; but in this case the wave was propagated in both directions: anteriorly in the usual manner, and posteriorly for a few segments as a direct peristalsis, as far as about the eighth segment from the hinder end.

The rate was in one case seen to be seven per minute.

Enchytraeus albidus Henle.

Here, again, the antiperistalsis, where it fails, does so at the hinder end, as is illustrated in the following two observations out of several:—

In one example antiperistalsis was absent in the last fourteen segments, was faint in front of this, and further forwards still was quite well marked. The rate of the contractions was five in two minutes, but the intervals were very irregular.

In a second specimen antiperistalsis began a short distance in front of the anus: the waves passed forwards slowly, traversing the high-power field of the microscope in twenty seconds, and the contractions were not very ample. Further forwards the waves increased in rapidity and strength; they were observed here to pass across the high-power field in ten seconds.

Fridericia bulbosa (Rosa).

This is the only Enchytraeid in which I have observed the reversed ciliary action in the gut which is so common in the other lower Oligochæta. I saw it in one specimen only, in the eighth and ninth segments from the hinder end. In front of this point, and behind it, ciliary motion could be seen, but it was indefinite in direction; it was not to be observed at all over the greater part of the alimentary canal.

Æolosomatidae.

Æolosoma viride Stephenson.

When I first described this form (46) I was inclined to think that it might be possible to unite it with *A. Headleyi* Bedd.; further study has, however, convinced me that differences of colour, of shape of the cerebral ganglion, of the number of nephridia, and especially of the form of the setæ, require that it should be considered as specifically distinct.

Antiperistaltic movements occur constantly, often at the rate of about forty per minute. The waves may include the stomach, as well as the whole length of the intestine; or, while some include the stomach, others may cease at its posterior end.

Ascending ciliary action occurs in the intestine, and is often very distinct and violent in its posterior part.

Æolosoma hemprichi Ehrbg.

In the form which I have tentatively identified as above (47), the antiperistalsis is commonly, though not always, confined to the dilated portion of the alimentary canal in about the middle third of the length of the animal, which may be called the stomach. In one case the antiperistalsis was obvious in the posterior two-thirds of the stomach, while a direct (antero-posterior) peristalsis occurred in the anterior third; the two waves meeting, the antiperistaltic overcame the direct wave, and then continued forwards to the anterior end of the stomach.

Ascending ciliary action also occurs in the intestine, and may be very distinct and violent, so as to be easily visible with the low power. Though as a rule confined to the posterior part of the alimentary canal, it may extend into the stomach; but often the ciliary motion in the stomach, though distinct, is indefinite in direction, or it may be antero-posterior. Small algal bodies may be carried upwards for a short distance along the alimentary tract, *i.e.* postero-anteriorly, by means of the ciliary current, and food-remains may also be swept in the same direction by the same force.

Experiments with carmine particles were made in an animal which was exhibiting violent ciliary motion. Particles were taken into the intestine through the anus by ciliary action, and were carried upwards for a short distance. They were then arrested, and moved alternately a little upwards and a little downwards for some time, and finally were quickly shot out through the anus. The antiperistaltic movements of the gut assisted the particles in ascending the intestine; but none ever seemed to get up for a distance of more than two or three times the diameter of the animal's body.

In this species I paid some attention to the motion of the food-matter in the alimentary canal. The contents of the intestine were often moved round and round in a rotatory manner about an axis coinciding in direction with the axis of the gut. This rotatory movement occurred while the cilia were working in the usual postero-anterior

direction, and does not seem easy to account for. It may, however, be suggested that the postero-anterior stream of water along the intestinal wall, occasioned by the ciliary movement, must have as its complement an antero-posterior axial stream of water returning to the exterior at the anus, 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; and it is possible that the rotation about an axis of the matter in the intestinal canal may be in some way due to the combined action of these two currents. HARMER (23) describes a rotatory movement of the fæces in the Polyzoa as being due to the intestinal cilia.

The fæces may pass out at the anus without the ascending ciliary action being suspended—a demonstration of the axial antero-posterior stream assumed above.

Summary.

The following list includes all the Microdrili which I have hitherto examined with reference to these phenomena; the occurrence of antiperistalsis and ascending ciliary action, or their absence, is noted against each:—

	Antiperistalsis.	Ascending Ciliary Action.
NAIDIDÆ—		
<i>Nais communis</i> Pignet, var. <i>punjabensis</i> Steph.	Yes.	Yes.
<i>Stavina punjabensis</i> Steph.	Yes.	Yes.
<i>Branchiodrilus hortensis</i> (Steph.)	Yes.	Yes.
<i>Pristina longiseta</i> Ehrbg.	Yes.	Yes.
„ <i>aquiseta</i> Bourne?	Yes.	Yes.
<i>Stylaria lacustris</i> (L.)	Yes.	Yes.
<i>Autophorus tonkinensis</i> (Vejd.)	Yes.	Yes.
<i>Dero</i> sp. i.	Yes.	Yes.
„ sp. ii.	Yes.	Yes.
<i>Nais paraguayensis</i> Mchln.	Yes.	?
<i>Naidium</i> sp.	Yes.	?
<i>Chætogaster punjabensis</i> Steph.	No.	No.
„ <i>orientalis</i> Steph.	No.	No.
TUBIFICIDÆ—		
<i>Limnodrilus socialis</i> Steph.	Yes.	Yes.
<i>Clitellio arenarius</i> (Müll.)	Yes.	Yes.
<i>Branchiura sowerbyi</i> Bedd.	Yes.	No.
ENCHYTREIDÆ—		
Numerous species	Yes.	No.*
ÆOLOMATIDÆ—		
<i>Æolosoma viride</i> Steph.	Yes.	Yes.
„ <i>hemprichi</i> Ehrbg.	Yes.	Yes.

* Except in a single specimen of *Fridericia bulbosa*.

Exceptions to the General Rule.

On a perusal of the foregoing table it will be seen that a number of the lower Oligochaeta exhibit in general the phenomena of antiperistalsis and ascending ciliary action in the intestine. All the species observed, except those of the genus *Chatogaster*, show antiperistalsis; all except the Enchytraeidae, *Branchiura sowerbyi*, and the genus *Chatogaster*, show ascending ciliary action.

Branchiura sowerbyi is one of the few Oligochaeta which possess gills. It is true that certain Naididae (*Dero*, *Aulophorus*, *Branchiodrilus*) have, in addition to branchial respiration, an ascending ciliary current in the intestine. Still, it seems not improbable that in *Branchiura sowerbyi* the presence of branchial may be correlated with the absence of intestinal respiration.

With regard to the Enchytraeidae it is to be observed that, though included in the present investigation for reasons which will appear more fully in the next section, they are by no means strictly, or even predominantly, of aquatic habit. I have only twice obtained single immature specimens (probably of a species of *Enchytraeus*) with a net when exploring the aquatic vegetation of tanks at Lahore; but Enchytraeids are to be found in profusion, for example (at least in Europe), under stones along the seashore, on both sides of the upper tide limit; or under stones that have been lying for some time undisturbed almost anywhere; or in moist ground. Some are plant parasites; others are found in dung-heaps. They cannot live in absolutely dry ground; but the immense numbers that exist in the soil may be illustrated by some figures given by BRETSCHER (10). This observer found a sample of earth to be entirely devoid of Enchytraeids on one occasion only; in other cases numbers varying from 4 to 615 were found in about two square decimeters of ground.

The phenomenon of ascending ciliary action can only be of use for respiratory purposes where the animal lives in water; and since this is not the case with the majority of Enchytraeids, and perhaps was not the case with the ancestor of the family, it is not to be expected that it should occur amongst the existing members of the group. The ascending peristalsis, as has already been noted, and as will be further shown in the next section, subserves the circulation; and hence, though its original import, according to the view here taken, was probably respiratory or alimentary, it has been retained, and is found regularly throughout the group.

On the possible Descent of Chatogaster from Parasitic Ancestors.

The case of *Chatogaster* remains to be considered. This is perhaps the most remarkable genus of the Naididae; and VEJDovsky (54) separates it as a distinct family. Later writers have not followed this example; but whether or not the characters of the genus are deemed sufficiently distinctive to justify this course, it must be admitted that the Naididae are its nearest relatives. Now the other genera of the Naididae appear, so far as yet observed, to show regularly both of the phenomena here under

discussion ; and it is therefore of interest to speculate as to the reasons for the remarkable exception in the case of *Chatogaster*.

Supposing, as has been done throughout, that the phenomena of antiperistalsis and ascending ciliary action are respiratory in purpose, their absence in this genus might be due to the present or past occurrence of conditions of life which do not or did not permit of this means of respiration—that is, to life in a medium other than water. Two such possibilities present themselves—a terrestrial, or a parasitic existence. While there is no reason for thinking that the present-day forms are descended from terrestrial ancestors, there are, on the other hand, certain facts which seem to point towards a parasitic habit in the past.

In the first place, one species, *C. limnæi*, may actually be found as an endoparasite in the liver of certain Pulmonata, while others of the same species live on the surface of the same water-snails. Other species of the genus, though not parasitic, may live as commensals ; thus *C. bengalensis* was usually found by ANNANDALE (1) clinging by means of a posterior sucker to the external surface of the body or to the edge of the shell of water-snails (*Limnæus*, *Limnophysa*, etc.), sometimes entirely withdrawing within the shell when disturbed ; this species may also, however, be free-living. The same observer (2) found *C. spongillæ* living in *Spongilla carteri*, and again on the surface of a variety of *Plumatella repens* ; while another species of *Chatogaster* also lives on the same *Plumatella*.

Secondly, the carnivorous habit is characteristic of many, perhaps of all, members of the genus. I found (46) in the alimentary canal of *C. orientalis*, small Crustacea, rotifers, small nematodes, *Paramacium* and other Ciliata. Setæ were often found in the crop, probably belonging to specimens of *Nais communis* which had been digested. On one occasion I found several individuals exploring with their mouths the surface of a dead and decomposing fly ; on another, I observed for some time the efforts of a *Chatogaster* to engulf in its distensible pharynx a Daphnid, which was, however, far too large to be thus disposed of. *C. bengalensis* (ANNANDALE, *loc. cit.*) devours small Crustacea ; *C. spongillæ* eats the dead and decaying parts of the sponge in which it lives ; a third species observed by ANNANDALE feeds on Protozoa (*Vorticella*, *Epistylis*, *Stentor*, etc.) ; ANNANDALE, however (1), mentions having had an English species sent to him in which the food probably consists of diatoms and the like. Since the Naididæ in general are vegetable feeders, it seems not unlikely that the carnivorous habit of the genus *Chatogaster* may be a remnant of a previous parasitic mode of life.

Under this head, along with the generally carnivorous habit, may be mentioned the modification of the anterior, or both anterior and posterior (ANNANDALE, 1), extremities of the body in some species to form suckers ; and the powerful pharynx, much larger, and attached to the body-wall by much more numerous and regularly radiating muscular strands, than in other Naididæ. In the other Naididæ also, the mouth is a transverse slit on the ventral surface, some distance behind the anterior tip of the body ;

and a tubular "buccal cavity" intervenes between mouth and pharynx. In *Chatogaster*, the large circular mouth reaches to the anterior end of the body (a prostomium being practically non-existent), and opens immediately into the barrel-shaped suctorial pharynx.

Thirdly, the absence of dorsal setæ, and reduction of the number of ventral setal bundles. The dorsal setæ, which in the other Naididæ are frequently much elongated, being as long as or sometimes much longer than the diameter of the body, would be detrimental to the success of an internal parasite by very considerably restricting its movements. The ventral setæ also are absent over a considerable region in the anterior part of the animal (segments iii.-v.). In *C. orientalis* the setæ of segment ii., which are longer than the rest, are directed anteriorly, not perpendicularly to the body-wall; the ventral setæ in this species are "somewhat small compared with the size of the animal." Such conditions, as more readily allowing of movement within the body of the host, would be of advantage to an internal parasite.

Fourthly, the incompleteness of the dissepiments. This is illustrated by the fact that no sperm- or egg-sacs are formed, and that sperm-morule ripen in the general body-cavity, passing freely from one part of the body to another, even to the posterior end of the last animal of a chain (48). This may be paralleled by the absence or incomplete development of the dissepiments in boring Polychætes, and by their incomplete development at the anterior end in earthworms. This character is useful, inasmuch as it allows the anterior end of the animal to be made firm and resistant by being distended with coelomic fluid, and it may, in the present instance, be correlated with previous boring habits of parasitic ancestors.

The commencing disappearance of the vascular system in the anterior part of the body in *C. crystallinus* (VERBOVSKY, 54), and the entire absence of external annulation in the genus, are also perhaps worthy of mention in this connection.

There are thus a number of features, peculiar to *Chatogaster* alone among the genera of the Naididæ, which seem to point to the existence of a parasitic mode of life in the ancestors of living forms, or which at least are consonant with such a supposition. If we accept this view, it is easy to understand the absence of antiperistalsis and ascending ciliary action in the intestine in this genus; these functions, existing originally in this as in other genera of Naididæ, were given up on the assumption of the parasitic habit; and consequently are no longer found, though the genus has returned almost completely to a free-living existence.

It is possible that *Chatogaster* does not stand alone in having returned to a free life, and a parallel is perhaps to be found among the Nematodes. I quote the views of HATSCHKE and HUBRECHT, as given by RAUTHER (39A):—"Es ist fraglich [he is quoting HATSCHKE] ob die parasitischen oder die freilebenden Nematoden dem Ausgangspunkt der Gruppe näher stehen. Man möchte der ersteren Vermuthung den Vorzug geben und annehmen, dass viele Eigentümlichkeiten dieser aberranten Thiergruppe durch den Parasitismus erworben worden sind, doch spricht auch manches für die zweite Theorie.

. . . HUBRECHT bemerkt, dass ihm 'der Versuch immer als ein verfehlt erschien ist, die parasitischen Nematoden sich hervorgegangen zu denken aus den frei im süßen Wasser, im Meere und in der Erde lebenden.' Letztere hätten sich sekundär an die freie Existenz adaptiert."

Summing up the present section, we may conclude that phenomena which point to the intestine as a respiratory organ of some importance occur very commonly among the aquatic Oligochæta; the genus *Chaetogaster* forms a remarkable exception to the general rule—an exception which it is proposed to explain by assuming the descent of existing forms from endoparasitic ancestors.

2. THE CONTRACTIONS OF THE ALIMENTARY WALL IN THE AQUATIC OLIGOCHÆTA IN RELATION TO THOSE OF THE VASCULAR SYSTEM.

I propose in the present section to consider the relations which exist, in a certain number of the forms previously mentioned, between the postero-anterior contractions of the alimentary wall and the postero-anterior contractions of the intestinal vascular network, or of the dorsal vessel of the circulatory system. For this purpose I shall take the various forms in the order which seems to me best calculated to bring out what I consider to be the meaning of the phenomena described.

It will be necessary to mention the chief features of the circulatory system in a number of these forms; but into the much-discussed questions of the histology of the walls of the blood-channels, and of the exact situation of these latter in respect of the several component layers of the wall of the intestine, I shall not enter.

VEJDOVSKY (53), in describing the antiperistaltic movements of the intestinal wall in Enchytræids, describes also how these movements propagate themselves forwards, beyond the point where the dorsal vessel arises from the intestinal sinus, as the postero-anterior contractions of the dorsal vessel. I have not met with any other observations of a similar nature.

Eolosomatidæ.

Eolosoma hemprichi Ehrbg.

Anatomy of Circulatory System.—In the form which I have identified as *Eolosoma hemprichi* (46) there is no separate dorsal vessel in the region of the intestine, but the intestinal wall contains a system of vacuole-like lacunæ. This lacunar system extends throughout the stomach also, but in this region a small though distinct dorsal vessel makes its appearance, the cavity of which is traversed by strands. The vascular channels are continued forwards dorsally on the œsophagus by a wide, thin-walled vessel which appears as if made up of a number of apposed vacuole-like chambers, or as a single elongated chamber traversed by numerous strands or septa. In front of the œsophagus this becomes a definite blood-vessel with a clear uninterrupted lumen, extending

forwards as far as the base of the cerebral ganglion, where it bifurcates. The branches are continued downwards and backwards on the wall of the buccal funnel to unite in the ventral vessel, which is intimately connected with the alimentary canal for the greater part of its extent, appearing on the intestine as a median ventral sinus of the intestinal wall, and at the posterior end of the animal losing itself in the vacuolar spaces of the gut-wall.

Relation of Contractions of Vascular System to those of the Alimentary Canal.—The vacuole-like spaces in the intestinal wall are occluded by the passage of the antiperistaltic waves, which, as they pass along, constrict at the same time the lumen of the gut. The vascular network, however, may at times be seen to be independently contractile in a postero-anterior direction; that is, the diameter of the lumen of the gut may be quite unaffected, so that it is impossible to speak of an antiperistalsis of the gut-wall, each contraction, as it passes along, merely occluding the lacunæ. In still other cases the movements might be interpreted either as contractions of the vascular network, or as a feeble antiperistalsis of the gut-wall—since the waves, in addition to emptying the network as they pass, cause also a slight constriction of the lumen of the intestine; and the various grades of the phenomenon seem to shade into each other.

There is often a definite relation in time between the antiperistalsis of the stomach and the postero-anterior contractions which pass along the “heart,” as the dorsal vessel* on the œsophagus may be named; in the sense that these latter seem to be a continuation forwards of the former—that the antiperistaltic wave, arrived at the anterior end of the stomach, occasions the contraction of the “heart,” which thus follows it up and seems to be its extension forwards. But this relation is by no means constant. Thus—

(1) The contraction of the “heart” may not follow on every antiperistaltic wave, but may occur after about every second wave.

(2) Or, after following regularly on the antiperistaltic wave for some time, it may then tend to anticipate the arrival of the latter.

(3) Or, while still occurring definitely in a postero-anterior direction, the contractions of the “heart” may be quite independent of the antiperistaltic waves in the stomach both in time and rhythm. They may be far more numerous, *e.g.* about five contractions of the “heart” for every antiperistaltic wave in the stomach wall.

(4) Or again, the direction of the contractile wave through the “heart” may in some cases be definitely antero-posterior instead of, as usually, the reverse.

In *Eolosoma hemprichi*, then, a condition exists in which the circulatory system is in close relation with the alimentary, appearing in far the greater part of its extent as a component part of the alimentary wall. Even on the œsophagus the dorsal vessel retains traces of its origin as a specialised channel in a system of vacuole-like spaces, since it shows us a lumen traversed by strands or incomplete septa.

* Cf. VEJDovsky (54, p. 21), “The dorsal vessel appears as a large, strongly pulsating heart.”

Physiologically, also, the contractile activities of the two systems are closely connected. In the middle and posterior parts of the animal, the contractions of the two systems are fundamentally the same thing, a somewhat feeble contractile wave affecting only the vacuole-like spaces of the circulatory system, while a stronger contraction of the same nature manifests itself as an antiperistaltic wave of the intestine. And where, in the oesophageal region, the two systems are becoming anatomically and physiologically differentiated from each other, there is still a want of definiteness about the result, as evidenced by the difference at various times in the direction of the "heart's" contractions, and in the relation of these to those of the muscular wall of the stomach.

VEJDOVSKY (54, p. 21) describes certain "shining spindle-like bodies, appearing to consist of single cells," which are shown by him in his pl. i. fig. 5, as oval or spindle-shaped cells, suspended in the middle of the lumen of the "heart" by fine strands attached at each end to its dorsal and ventral walls respectively. They are doubtless the same as the strands or septa traversing the lumen of the "heart" which I have mentioned above.

It is presumably to these strands that BEDDARD (3, p. 180) refers when he says: "In several species there is a row of somewhat fusiform cells in the dorsal vessel, which have yellowish fat-drops in their interior. I have suggested that these cells probably represent a rudimentary dorsal organ such as is found in the Enchytræidæ."

Now the dorsal organ, or cardiac body, of the Enchytræidæ is a cellular rod attached to the ventral side of the dorsal vessel and appearing in a transverse section as a mass of cells projecting into the lumen of the vessel from its ventral side, and not attached at all to the dorsal wall of the vessel; this structure, BEDDARD considers, may have originated from a dorsal diverticulum of the gut, comparable to the paired dorsal diverticulum of *Buchholzia*, which has become solid. It does not, however, seem easy to compare a number of isolated strands, traversing the whole lumen of the vessel, and attached to its dorsal as well as its ventral wall, with a solid cell mass projecting upwards from the ventral wall and having no attachment to the dorsal wall of the vessel.

An alternative view has been indicated above. Regarding, with VEJDOVSKY (54, p. 115), the vascular network of the intestine as the principal component of the vascular system of the Oligochaeta; and recalling the fact that in the Aeolosomatidæ and Enchytræidæ the vascular network or sinus is present alone in the intestinal region, while in other families a dorsal vessel is present in addition, it seems permissible to regard this vessel, in the families where it occurs, as a differentiation, a specialised track, of the network. On this view the strands passing across the lumen of the "heart" of *Aeolosoma* would be conceived as vestiges of the partitions existing in an original lacunar system; and the presence of the strands would be an argument for the primitive character of *Aeolosoma*—not, as on BEDDARD's view of their nature, an argument in the contrary sense.

Aelosoma viride Stephenson.

Anatomy of Circulatory System.—This agrees with what has been stated for *A. hemprichi*, with the exception that the dorsal vessel has attained a somewhat higher degree of differentiation. A definite dorsal channel can sometimes be distinguished in the alimentary wall as far back as the anterior part of the intestine; and the dorsal vessel in the œsophageal region ("heart") is throughout its length always a definite tube, with a clear lumen uninterrupted by strands.

Relation of Contractions of Vascular System to those of the Alimentary Canal.—The relation of the contractions of the system of vascular spaces in the gut-wall to the antiperistalsis of the alimentary tract is the same as that which obtains in *A. hemprichi*. The dorsal vessel, where it appears as a channel in the alimentary wall, is not independently contractile apart from the movements which take place in the wall as a whole. The ventral vessel on the intestine is neither itself contractile, nor is its diameter at all affected by even well-marked antiperistaltic movements of the intestine; it would seem, therefore, though I have no direct observations on the point, that the vessel must lie outside the muscular layer of the intestinal wall.

The contractions of the "heart" furnish an interesting series of variations, in part analogous to those described above for *A. hemprichi*. The most usual condition, here as there, is that the contractions of the "heart" are postero-anterior in direction, and form a continuation forwards of the antiperistaltic waves of the stomach, recurring fairly regularly like these latter at intervals of a second, a second and a half, or two seconds. In addition, the following variations occur:—

(1) The contractions of the "heart," though recurring regularly, and at the same rate as the antiperistaltic contractions of the stomach, may not immediately follow on the arrival of the waves at the anterior end of the stomach, but may occur in the intervals between the arrival of two successive waves.

(2) The two rhythms may be partially or completely independent. As an example of partial independence, it was observed that if the antiperistaltic wave reaches the anterior end of the stomach shortly before a contraction of the "heart" is due, it evokes a contraction, and is thus continued forwards in the typical manner; if, however, the antiperistaltic wave reaches the anterior end of the stomach soon after the "heart" has completed a contraction, no effect is produced, the stimulus being apparently applied during a "refractory period."

(3) Instead of proceeding in a wave-like manner, the contraction of the "heart" may be practically simultaneous along its whole length.

(4) The contraction may be initiated not at the posterior end of the "heart," but at some distance, a third or a half of its length, from its posterior end; the contraction then spreads in both directions from this point, forwards along the anterior, backwards along the posterior part of the "heart."

(5) The contractions of the "heart" may be definitely antero-posterior in direction;

and when this occurs, one or several such antero-posterior contractions usually alternate with one or several in a postero-anterior direction. On one occasion a long series of antero-posterior contractions was observed during a period when the antiperistaltic movements of the stomach were in abeyance.

The conditions which exist in this form may be summarised as follows:—Anatomically, the degree of differentiation attained by the vascular system is rather greater than in the case of *A. hemprichi*, inasmuch as the dorsal vessel has lost the strands which pass across its lumen, and a definite dorsal channel may also be discoverable on the anterior part of the intestine. Physiologically, the contractions of the intestinal vascular network and the antiperistalsis of the gut are essentially the same phenomenon; and anteriorly where, in the oesophageal region, the “heart” has more fully differentiated itself from the alimentary wall, its contractions, while they may frequently be initiated by the antiperistalsis of the alimentary tract behind it, are in the absence of this relation irregular in rhythm and variable in direction; it is as if the contractile tissue of even this part of the circulatory system had not yet become habituated to independent action.

ENCHYTRÆIDÆ.

In the Enchytræidæ, the main portion of the circulatory system is represented by a close network of vessels in the intestinal wall, the intestinal plexus or so-called perienteric sinus. In the posterior part of these worms, there is no dorsal vessel; but at or near the anterior end of the intestine the intestinal plexus comes to an end, and the dorsal vessel arises, continuous at its origin with the anterior end of the plexus. The dorsal vessel bifurcates anteriorly, the branches being continued downwards and backwards, and uniting to form the ventral vessel. There are a number of lateral commissural vessels in the anterior part of the animal which join the dorsal and ventral vessels. The ventral vessel is continued backwards to the posterior end of the body; it does not enter the intestinal plexus, but is a distinct vessel, lying either on the gut or separated from it by numerous “windows,” as far as the hinder end. The dorsal vessel is contractile, the ventral not.

The relations of the alimentary and vascular contractions in the Enchytræidæ may be illustrated by observations on a worm belonging to this family, which I examined in Lahore some time ago. Enchytræids are not common in India, and this specimen not being sexually mature it was impossible to identify it; it probably, however, belonged to the genus *Enchytraeus*.

The dorsal vessel arose from the gut plexus in the twelfth segment, and could be followed, attached to the wall of the alimentary canal, as far forwards as segment iv. The antiperistaltic contractions of the intestine, which are here and throughout the Enchytræidæ the means by which the blood is moved along the channels in the intestinal wall, were sluggish and of small amplitude; on arriving at segment xii. the contractions of the gut were after a momentary halt taken up by the dorsal vessel; the contraction of

the dorsal vessel then proceeded rapidly forward,—much more rapidly than the gut contraction, which originated it, had travelled along the intestine. The frequency of the two waves was, of course, the same, the one following on the other in quite regular sequence.

The difference in character of the two waves, or rather of the two portions of the same wave, was striking; the one sluggish, a general antiperistalsis of the whole gut; the other rapid, confined to the dorsal vessel. Equally striking was their interconnection or mutual dependence, the antiperistalsis being regularly continued forwards by the postero-anterior contraction of the dorsal vessel.

Of specimens subsequently observed at Millport, most merely repeated in essentials the phenomena just described. A few variations may be recounted.

In *Lumbricillus tuba* (50) the contraction of the dorsal vessel is usually, as in other forms, a simple and direct continuation of the antiperistalsis of the intestine; there is no break of continuity, and the alimentary and vascular contractions may be looked on as two parts of the same phenomenon. In one specimen, however, where the dorsal vessel began in segment xiii., the antiperistaltic wave sometimes stopped short at segment xv., so that segment xiv. formed a break between the two, and the contraction of the dorsal vessel was not then directly continuous with the antiperistaltic contractions of the gut. In another case the correspondence between the arrival of the antiperistaltic wave and the beginning of the contraction of the dorsal vessel was not absolute; a vascular contraction might be intercalated between the arrivals of two successive antiperistaltic waves; or the beginning of the contraction of the dorsal vessel might slightly anticipate the arrival of the antiperistaltic contraction. The most interesting specimen, however, was one in which the antiperistaltic waves and the contractions of the dorsal vessel were both regular, but the rhythm of the two was not quite the same; the contractions of the dorsal vessel were a little more frequent, and thus for a short time now and then the vascular would seem to be a continuation of the alimentary contraction; but a longer observation shows that they were really independent.

In the foregoing species the want of unity between alimentary and vascular contractions is only occasional; in *Enchytræus albidus* it seems to be more fundamental. In two examples of this species the contraction of the dorsal vessel was independent of the arrival of the antiperistaltic wave; the dorsal vessel pulsated several times for each antiperistaltic wave which reached the anterior end of the intestine. In another specimen the dorsal vessel originated in segment xvi.; the antiperistalsis stopped abruptly at xvii., and there was an interval of a segment which showed no pulsation of any kind; the contractions of the dorsal vessel were often quite independent of the arrival of the wave behind it; the rate of the antiperistaltic contractions was only five in two minutes, and the rhythm was irregular, while the dorsal vessel, on the contrary, was contracting regularly four times per minute. The absence of any kind of contraction in the space of a segment between the point where antiperistalsis ended and where the dorsal vessel began was noticed in another case also.

Summing up the condition in the Enchytræidae, we may say that both anatomically

and physiologically the state of things is much as in *Kolosoma*. The circulatory system is anatomically on a somewhat higher level, since it possesses a series of lateral commissural vessels in the anterior part of the body; it however maintains its close relation with the alimentary system, appearing in a large portion of its extent as a part of the alimentary wall; the dorsal vessel is a forward continuation of the gut-plexus. Physiologically, the blood is moved, in the region of the intestine, by postero-anterior contractions of the alimentary wall; and anterior to this these contractions are continued forwards as the postero-anterior contractions of the dorsal vessel. Though in most cases the physiological unity of the contractions of the alimentary wall and of the anatomically independent dorsal vessel is unmistakable, there is in one observed case (*Lumbricillus tuba*) an occasional, and in another (*Enchytræus albidus*) apparently a more fundamental dissociation of the two.

NAIDIDÆ.

The Genus Chætogaster.

Chætogaster orientalis Stephenson.

Anatomy of Circulatory System.—In describing the *gut-plexus*, it is convenient first to distinguish the various parts of the alimentary canal. Behind a massive pharynx comes the narrow œsophagus, and to this succeed two considerable dilatations, which may be distinguished (46) as “crop” and “stomach”; behind the stomach the tube is continued as the intestine.

In the wall of the crop there is on each side a series of transverse parallel vessels, arising above from the dorsal vessel, and joining below a sinus-like channel in the mid-ventral line. These parallel vessels appear in an optical section of the wall as clear vacuole-like spaces; they are separated from each other by intervals which are equal in breadth to the diameter of the vessels themselves, and are connected with their neighbours on each side by fairly frequent and distinct cross channels. Similar parallel vessels occur on the stomach, connected with each other here also by cross branches; on the whole, however, the vessels are less regularly arranged and are fewer than on the crop. This condition is paralleled by the optical section of the stomach wall, the vacuole-like spaces being here, as compared with the crop, somewhat less conspicuous, less regular, and further apart from each other. On the intestine the vacuoles representing the vessels of the wall are still fewer than on the stomach.

The mid-ventral channel in the wall of the crop has already been mentioned. Anteriorly it loses itself in the network of the crop-vessels, without being connected with the ventral blood-vessel. Posteriorly it is continued on to the stomach as a broad channel, traceable backwards on to the intestine; but here, though definitely present, it is much less obvious.

The *dorsal vessel*, contractile as far forwards as the cerebral ganglion, is closely con-

neeted with the alimentary wall as far as the oesophagus; it is again attached to the dorsal surface of the posterior part of the pharynx, becoming free once more before it divides. It is continued as two lateral vessels, one on each side of the buccal cavity, which unite ventrally in the ventral vessel.

A pair of contractile *lateral commissural vessels* are present in the œsophageal region.

The *ventral vessel* is separated from the alimentary canal, with which, however, it is connected by a number of wide communications; these in the intestinal region, and presumably in the other regions also, pass from it to the mid-ventral sinus of the alimentary wall.

It will be remembered that in *Chaetogaster orientalis* and *C. punjabensis* the alimentary canal exhibits no antiperistaltic movements, and there is accordingly no question here of any relation between this phenomenon and the vascular contractility. I have nevertheless described the anatomy of the circulatory apparatus in the same way as has been done for previous forms, because the anatomical condition seems to form a link in a natural series.

There is, again, a well-marked gut-plexus, specialised here anteriorly into a regular series of lateral channels; but a dorsal vessel is here distinct throughout the length of the animal; a separate ventral vessel is present, independent of the gut-wall; and, in addition, there is a pair of contractile lateral commissures. The blood, as in the *Æolosomatidæ* and many *Enehytræids*, is colourless.

The subsequent argument may here be so far anticipated as to say that I propose to consider the vascular system in the Chaetopoda as a specialisation of and a development from a primitive lacunar network or plexus in the gut-wall; and the contractility of the vascular system, which throughout the group is manifested pre-eminently in a postero-anterior peristalsis of the dorsal vessel, as a derivative of the contractility of the alimentary canal; which latter is also, in the aquatic and presumably more primitive forms, in the greater portion of its extent a postero-anterior peristalsis.

I have previously given reasons for supposing that the genus *Chaetogaster* originally possessed a postero-anterior peristalsis of the gut, like its congeners; and that this disappeared during an endoparasitic stage in the history of the ancestors of present-day forms. I have here to remark, that though the general antiperistalsis of the gut-wall may be supposed to have disappeared during the parasitic stage, as being useless for respiratory purposes, it would nevertheless be perpetuated as far as regarded that longitudinal strip of the alimentary tube which contained the now differentiated dorsal vessel, in order to subserve its second function, the circulation of the blood; and hence we now have what is, in these aquatic forms, the anomaly of a contractile dorsal vessel with a quiescent gut-wall.

Other Naididæ.

The Naididæ in general show a very interesting transition stage in the relations of the contractions of the vascular system to those of the alimentary canal. In the families

previously discussed (*Æolosomatidæ* and *Enchytræidæ*) there is no differentiated dorsal vessel on the intestine; the whole of the intestinal plexus is contractile,—in this sense, that the blood spaces, being contained within the muscular coats of the alimentary canal, are emptied in a forward direction by the recurring antiperistaltic contractions of the alimentary wall. In the *Naididæ* a dorsal vessel is differentiated in the intestinal region; still however in close connection with the alimentary canal, indeed forming part of the alimentary wall, it is physiologically as well as anatomically one with the latter. The antiperistaltic contractions still persist, and move the blood in the dorsal vessel, as well as in the intestinal network; but the dorsal vessel shows nevertheless signs of a partial independence; contraction is frequently more marked, and more regular, along this dorsal strip of the canal than elsewhere. The actual phenomena vary from species to species; and a number of examples will illustrate the progressive differentiation or emancipation, anatomically and physiologically, of the vascular from the alimentary system.

The Genus Dero.

In the genus *Dero* the homologue of the dorsal vessel is situated on the ventral wall of the alimentary canal for the greater part of its length, and is closely united with the alimentary wall till within a short distance of the anterior end of the animal. A network of vessels exists in the intestinal wall, with, in one species examined by me, a longitudinal vascular channel in the median dorsal line (the true dorsal vessel, as said above, is situated ventrally). The ventral vessel is non-contractile, and separate from the intestine except posteriorly, where it becomes joined to the alimentary wall; it gives segmental branches to the intestine. There are a number of contractile lateral commissural vessels in the anterior part of the body.

Relation of Contractions of Vascular System to those of the Alimentary Canal.—Though the postero-anterior contraction of the dorsal vessel is usually merely a part of the antiperistaltic contraction of the intestine, the following observations may be cited as showing a commencing independence:—

(1) A strong and regular antiperistalsis was observed, with a rhythm of twenty-seven per minute, in the posterior part of one of these animals. Further forward, the intestinal walls took little part in the contractions, which thus here mainly affected the dorsal vessel. In the anterior component of this chain of two the participation of the intestinal wall became less and less, and ceased altogether at segment xiii. from the anterior end of the animal, the only motion visible in front of this being that of the dorsal vessel.

(2) In another specimen the dorsal vessel was contracting regularly at the rate of twenty-eight per minute; the walls of the intestine, though shaken by the passage of the successive waves, took no part in the contractions. Further forwards the contractile wave included the intestine also; the antiperistalsis was sufficiently violent to cause food matters in the intestine to be shot upwards for some distance on the passage of each wave.

Aulophorus tonkinensis (Vejd.).

The vascular system has been briefly described by me in a previous paper (49); it closely resembles that of *Dero*.

The antiperistaltic contractions of the alimentary canal were, in the posterior portion of one specimen examined, mainly confined to the portion of the wall containing the dorsal vessel; the opposite side of the intestine moved but little, *i.e.* the phenomenon manifested itself in this region principally as a postero-anterior contraction of the dorsal vessel. In the middle of the body, however, in segments xiii., xii., and xi., the whole circumference of the alimentary canal manifested a series of very violent antiperistaltic contractions. Later, it was observed that the slowly moving antiperistaltic pulsation, which embraced the whole intestinal wall, became transformed in segment xi. into an extremely rapid wave, which, affecting the dorsal vessel only, shot forwards through the rest of the field of the microscope almost instantaneously.

Thus in *Aulophorus tonkinensis* the same series of contractions may manifest itself at one place as an antiperistalsis of the whole gut, and at another place mainly as a contraction of the dorsal vessel. It may be remarked that the latter part of the observation detailed above is strongly reminiscent of the condition in the Enchytræidæ.

Slavina punjabensis Stephenson.

I have no detailed observations concerning the anatomy of the vascular system in this form. The opacity of the specimens, due to the adherent foreign particles, renders an examination of the details difficult or impossible. The dorsal vessel appears as a part of the wall of the intestine; and the ventral vessel is separated from the intestine, as in other Naididæ.

Relation of Contractions of Vascular System to those of the Alimentary Canal.—As in *Dero* and *Aulophorus*, the dorsal vessel in this form is never, so far as I have seen, independently contractile, apart from the rhythm of the gut contractions. The following observations will illustrate the nature of the relations between the two:—

(1) In a specimen which was preparing to divide, with eyes already forming in its posterior half, an ordinary typical antiperistalsis at the rate of twenty-five per minute was observed in the hinder part of the anterior animal of the chain; the dorsal vessel, as forming part of the intestinal wall, shared in the constrictions, and was emptied in a forward direction simultaneously with the passage of the waves. Further back, in the middle of the posterior animal, the phenomenon manifested itself mainly as a strong and swift contraction of the dorsal vessel; the ventral side of the intestine, however, was slightly indented as each contraction passed along. Further back still, near the hinder end of the posterior animal, the intestine took no share in the movement; the ventral wall showed no indentation on the passage of the contractile wave, which was confined to the dorsal vessel. We have, then, in such a case as this, a single contractile

rhythm affecting either one only, or both, of two associated structures, viz. dorsal vessel and intestine.

(2) At the hinder end of a chain of two animals a regular and strong antiperistaltic action, accompanied by a violent ascending ciliary motion, began at the anus; further forwards the contraction was mainly of the dorsal vessel, the opposite side of the intestine moving but little; and in the pharyngeal region of the posterior animal the contraction was solely of the dorsal vessel. Immediately consequent on the arrival of the wave at the anterior end of the hinder zooid, a contraction was initiated at the hinder end of the anterior zooid, but this now manifested itself as a typical antiperistalsis of the whole gut. I could not trace the continuity of the dorsal vessel through the region of approaching fission, and could not therefore see the actual continuity of each wave; but the time-relation described above was obvious and was observed for some time.

Nais communis Piguet, var. *punjabensis*.

Anatomy of Circulatory System.—There is a gut-plexus; and in the mid-ventral line of the intestine there is a median channel which is occluded as the antiperistaltic waves of the intestine pass along; the current in it must therefore be postero-anterior, as in the dorsal vessel.

The dorsal vessel, covered by chloragogen cells, appears as a part of the alimentary wall as far forwards as the œsophagus. It divides in the prostomium into two branches, which reunite ventrally to form the ventral vessel at the level of the setal bundles of the third segment. Four or five lateral vascular commissures are present in the pharyngeal region.

The ventral vessel is separate from the intestine except at the posterior end of the animal. There is a series of communicating vessels, of some width, though short, which pass, one in each segment, from the ventral vessel to the mid-ventral channel in the intestinal wall. Posteriorly the ventral vessel unites with this ventral channel a few segments in front of the anus, and ultimately is continued round the end of the intestine by a branch on each side; these meeting above form the origin of the dorsal vessel. The blood is red.

Relation of Contractions of Vascular System to those of the Alimentary Canal.—The dorsal vessel, where it is included in the intestinal wall, is affected by the antiperistaltic contractions of the latter, which cause a progressive postero-anterior constriction of the vessel as they pass along; the intestinal antiperistalsis and the vascular contractions are thus, in many cases at least, inseparable components of the same contractile wave. Certain variations, however, are sometimes observed:—

(1) Of a fairly regular series of contractions which are taking place in an animal under observation, some may affect the dorsal vessel only, others the lumen of the gut also. Or, during a period when antiperistalsis is temporarily in abeyance, the contractions of the dorsal vessel may proceed fairly regularly, perhaps at the rate of about

nine per minute; but at intervals an antiperistaltic wave may come along, obliterating the dorsal vessel in its progress, and thus combining the two series of phenomena in itself. The antiperistalsis appears to be the same thing as, although in a more violent form than, the contraction of the dorsal vessel.

(2) An antiperistaltic wave, beginning at the posterior end of the body as a constriction of the lumen of the intestine, may as it passes forwards become merely a contraction of the dorsal vessel; so that anteriorly, while the dorsal vessel is quite occluded by the passage of the wave, there is no, or only the very slightest, constriction of the lumen of the gut. Not only so; but we may have a contraction which, as it enters the microscopic field, has the characters of an antiperistaltic wave; the wave will cease to affect the lumen of the gut, and the ventral wall of the gut will not move, —in other words, the wave passes across the centre of the field as a contraction of the dorsal vessel; finally, the whole gut will again be constricted by the wave, *i.e.* the definitely antiperistaltic character of the phenomenon will be manifested by the participation of the ventral wall of the intestine in the constriction, and the wave will disappear from the microscopic field as an antiperistalsis once more. That is to say, that even in the same high-power field one and the same wave may be an antiperistalsis of the gut, a simple contraction of the dorsal vessel, and an antiperistalsis again.

The above series of observations, though representing variations from what may be regarded as the simpler and more typical condition, merely serve to emphasise the fact that the two series of occurrences are essentially manifestations of the same phenomenon. Other observations, however, illustrate a commencing tendency to dissociation of the two series, and show that the contractility of the dorsal vessel is becoming, in a slight degree, independent of the rhythm of the contractions of the alimentary wall.

(3) In certain cases, though antiperistaltic movements are going on, they do not seem greatly to affect the lumen of the dorsal vessel. The proper contractions of the dorsal vessel are less frequent than the antiperistalsis; in one case they coincided for a short time now and then with every second antiperistaltic wave, and in the intervals had a rhythm entirely their own. The impression here given was that of an essentially double series of events sometimes coinciding; not, as in previous cases, of an essentially single series sometimes differentiating into two.

(4) In one case the rhythm of both was the same in the posterior part of the animal, while anteriorly in the neighbourhood of the stomach the two series were independent.

In the four genera which have just been considered, the vascular system shows a greater degree of anatomical differentiation than in those previously discussed. The gut-plexus is a less marked feature; the general plan of the circulation, with distinct dorsal and ventral vessels, is as in *Chaetogaster*, but the contractile lateral commissural vessels are more numerous. The blood is red.

Physiologically, the contractility of the dorsal vessel is closely related to that of

the gut-wall of which it forms part; but anteriorly the continuation of the dorsal vessel, and also the lateral loops, manifest contractility, though not in anatomical association with the alimentary tube: and occasionally in *Nais* the dorsal vessel assumes an independent contractility even in the region of the intestine.

Branchiodrilus hortensis (Stephenson).

In this species (48, 51A) the dorsal and ventral vessels have much the same characters as in *Nais*. Besides branching vessels to the body-wall, there are present in each segment a pair of lateral loops, which in the anterior part of the body extend into the gills, the limbs of the loop forming the afferent and efferent vessels of these organs. The afferent vessel, springing from the dorsal vessel, is in this part of the body contractile; further back, where the branchial processes are small, the lateral loops do not extend into them, and no part of the loops is contractile; the lateral loops exist, however, though much reduced in size, as far back as the hinder end of the animal. In the first five segments the lateral vessels do not present the appearance of regular loops, but form an extremely irregular and complicated plexus. The blood is yellowish-red.

Relation of Contractions of Dorsal Vessel to those of the Alimentary Canal.—The contractions of the dorsal vessel are in this form independent of those of the intestine to a much greater degree than in any of the forms previously considered.

The dorsal vessel may contract regularly without any accompanying diminution of the lumen of the alimentary canal; conversely, intestinal antiperistalsis may proceed without occluding the lumen of the dorsal vessel.

The two series are, as a rule, independent in rhythm; thus the dorsal vessel may be contracting thirty-two times, and the intestinal walls only seven times per minute; or the dorsal vessel may contract thirty-six, and the intestine only eighteen times per minute. And here, though the rate of one was just double that of the other, the two never coincided; the character of the contractions also was different in the two series, the wave of contraction of the dorsal vessel passing along much more swiftly than that of the alimentary canal; the antiperistaltic wave recurred at regular intervals, the contractions of the dorsal vessel rather irregularly.

The two series may also be independent as regards the violence of their contractions. The dorsal vessel may contract actively while antiperistalsis is going on but feebly. Antiperistalsis may be quite absent in the anterior part of a specimen, while the vascular contractions in the same region are proceeding vigorously. An indication of some slight connection between the two series was however afforded by a specimen in which the vascular contraction often seemed to precede by about half a second the antiperistaltic wave of the intestine.

Anatomically, the vascular system here differs from that of the other Naididæ in the presence of lateral loops throughout the body, and in their extension, in the

anterior part of the body, into the gill-processes. The system may be said to have reached a higher stage of development, and a greater degree of independence of the alimentary canal, than in the preceding forms.

Physiologically, the advance shown by the present form over those immediately preceding, though it belongs like them to the Naididæ, is greater than that between any other two successive forms in the series here presented. Whereas hitherto the main feature has been the interconnection of the two series of contractions, here, on the other hand, their independence is strongly marked. In the preceding forms the gut contractions appeared to be the primary phenomenon, of which the vascular contractions were frequently merely a part; here, however, the vascular contractions are the more numerous, and begin to take the lead.

TUBIFICIDÆ.

Clitello arenarius (Müll.).

The circulatory system of this species has not hitherto been investigated in detail; it is probably, however, not very different in essentials from that of such a Tubificid as *Limnodrilus* (*vide post*). According to my observations the ventral vessel is continuous throughout the body; the suprainestinal vessel extends from segment vi. anteriorly to xii. posteriorly. The hearts are two pairs, in segments viii. and ix., and arise from the suprainestinal above, joining the ventral vessel below. The lateral commissures, segmentally arranged, exhibit in the posterior part of the body complicated windings, and penetrate the muscular coats of the body-wall so as to lie, in part of their extent, underneath the epithelium; but they are single continuous vessels and do not anastomose. In front of the middle region of the body they become progressively smaller and ultimately indistinguishable (at segment xxii. in an animal of 94 segments); in the anterior five segments of the body they again form a series of complicated loops.

Relation of Contractions of Dorsal Vessel to those of the Alimentary Canal.—Antiperistalsis, as previously stated, is always to be observed in this species, and its relation to the contraction of the dorsal vessel is interesting and suggestive. The latter may be illustrated by the recital of a number of observations.

Thus in one case antiperistaltic contractions began in the segment in front of the anus; passing forwards, each became, in the sixth segment above the anus, a contraction of the dorsal vessel only. In another case also, each contraction was a typical antiperistalsis of the gut at the posterior end of the animal; the waves gradually changed their character while passing forwards, and at the thirteenth segment from the hinder end each became merely a contraction of the dorsal vessel; no antiperistalsis was seen higher up the alimentary canal, either along with or independent of the vascular contractions. In still other cases the same kind of phenomenon was observed, the contraction being an antiperistalsis of the gut throughout the hinder segments of

the body, and a postero-anterior contraction of the dorsal vessel in front of this. In one case the contractile wave was throughout mainly a vascular contraction, *i.e.* affected principally the dorsal vessel; though in about the hindmost ten segments of the body the lumen of the gut appeared to be slightly diminished in calibre as the wave passed along, *i.e.* the wave was to a slight extent also an antiperistalsis of the gut.

At the risk of insisting on the obvious, I should like to point out how the observations on this species illustrate the essential unity of the vascular and alimentary contractions—how, as has been said before, they are fundamentally the same thing.

Limnodrilus socialis Stephenson.

I have previously (51) given a detailed account of the anatomy of the circulatory system in this species. The chief points are as follows:—

The dorsal vessel, ventral in position, as in *Dero*, for the greater part of its course, is situated in close contact with the intestinal wall, and is surrounded by chloragogen cells as far forwards as segment ix.; it then separates from the alimentary tube and becomes free in the body-cavity; it is contractile throughout its length. A supra-intestinal vessel is also present, as in many Tubificidæ; it is covered by chloragogen cells, and extends forwards as far as segment v., backwards to septum 8/9, where it enters a sinus-like space on the dorsal side of the intestine in the anterior part of segment ix. A large channel on the right side of the intestine, also covered by chloragogen cells, communicates anteriorly with the sinus in ix., and dies away posteriorly at about segment xxi. The intestinal plexus extends throughout the length of the intestine, and reaches as far forwards as iv.; the two last-mentioned vessels (but not the dorsal vessel) appear in sections as special channels of this network.

The hearts are a single pair in segment viii.; their pulsations have no definite time-relation to the contractions of the dorsal vessel from which they originate above; there is also a pair of long contractile loops to the genital organs. There are lateral commissural loops throughout the body, and these in the posterior part of the body give origin to branches which go to form the cutaneous plexus; these branches divide and anastomose freely, penetrating the muscular coats and coming to lie between the cells of the surface epithelium.

The ventral vessel in the anterior part of the body narrows rapidly behind segment vii.; it may apparently either die away on the intestine, or be continued as a narrow channel to join the ventral point of union of the two hearts. The junction of the hearts may be looked on as the origin of the main ventral vessel, which extends from this point to the posterior end of the animal; it is less intimately united to the intestine than is the dorsal vessel, and is not covered by chloragogen cells.

Relation of Contractions of Dorsal Vessel to those of the Alimentary Canal.—The antiperistaltic movements observed in this species were always quite unconnected with the contractions of the dorsal vessel. The latter were much more frequent, and also

much more rapid in their rate of progress. The passage of the wave in the dorsal vessel had no effect on the intestine, nor did the antiperistalsis of the intestine in any way affect the lumen or the contractions of the dorsal vessel. Further, antiperistaltic movements are frequently altogether absent, while the vascular contractions are always to be observed.

Branchiura sowerbyi Bedd.

The circulatory system in this species has been described by BEDDARD (3A), and also by me (51). The following are the chief points in its anatomy:—

The dorsal vessel is here also ventrally or ventrolaterally situated in the greater part of its course; it does not lie immediately on the intestinal wall, but has nevertheless a closer relation to the gut and to the chloragogen cells than has the ventral vessel. The suprainestinal vessel reaches the sixth segment anteriorly, and posteriorly ends at a point not far behind segment xii.; it is throughout in close relation to the gut and its chloragogen cells. There is a rich intestinal plexus in the gut-wall, which in segments x.—xiii. becomes almost a sinus; besides having connections with dorsal and ventral vessels, the plexus is joined to the suprainestinal by a series of wide communications.

The hearts are two pairs, in ix. and x.; the first pair originate above from the suprainestinal, and unite below to form the ventral vessel; the second pair arise above from the dorsal vessel, and enter the ventral vessel below. In segments ii.—viii. there is a series of non-contractile lateral loops, which give branches to the body-wall; the loops in viii. originate above from the suprainestinal, in the other segments from the dorsal vessel. Behind the hearts, and in front of the gills, the lateral loops are two pairs per segment; in the gill region the distribution is complicated. The parietal vessels, which originate from the loops, form a plexus in the body-wall; but no capillaries enter into the surface epithelium.

The ventral vessel of the anterior part of the body disappears on the ventral surface of the alimentary canal about segment ix. (cf. *Limnodrilus*); the main ventral vessel of the body is formed anteriorly by the union of the hearts, and is continued back to the posterior end of the animal.

Relation of Contractions of Dorsal Vessel to those of the Alimentary Canal.—The two series are independent. My observations may be summed up by saying that the dorsal vessel contracts regularly, rapidly, and frequently; the antiperistaltic waves sometimes intermit for a period, when present progress only slowly, and are much less frequent than the contractions of the dorsal vessel.

In considering the Naididæ (exclusive of the genus *Chatogaster*), an advance in the degree of differentiation of the vascular system, as compared with the *Æolosomatidæ* and *Enchytræidæ*, could be followed through such a form as *Nais* to *Branchiodrilus*, the end term of the series. This advance is manifested in a greater degree of

independence of the alimentary canal; the intestinal network becomes a less prominent portion of the whole system, and lateral loops, parietal vessels, and branchial vessels are developed. The physiological independence of the two systems also increases hand in hand with the anatomical; in the lower stages there is one series of postero-anterior contractions common to the two systems, while in the higher a separate series of vascular contractions is becoming differentiated from the alimentary series.

The Tubificidæ present us with further stages in this differentiation of the two systems. The anatomical summaries given under the headings of the three species here described show two things: first, that the degree of complexity attained by the vascular system is considerably greater than in such a typical Naid as *Nais*; secondly, that *Clitellio*, in having a continuous ventral vessel throughout the body, in possessing lateral loops which do not branch, and in being without either a cutaneous plexus or a system of branchial vessels, is at a lower level than the other species. The physiological observations correspond; they show that in *Clitellio* a very distinct connection between alimentary and vascular contractions is still to be observed—the degree of independence of the two being, in fact, less than in the Naid *Branchiodrilus*; but they show also that in the species with a still more developed vascular system, the alimentary and vascular contractions are now at length entirely independent of each other. The common contractility of the intestinal wall and included vascular elements has become differentiated into two parts—that of the alimentary wall, and that of the dorsal vessel. The character of the contractility possessed by these two structures is not the same: that of the dorsal vessel is the more marked, being more energetic, more frequent, and more rapid; while the contractility of the intestine seems to be losing in importance, since it is frequently absent, and when present, is more limited in extent than in the Æolosomatidæ, Enchytræidæ, and Naididæ.

Higher Oligochæta.

A full description of the vascular system in the earthworms need not be given; as is well known, and as may be illustrated by the description given by FUCHS (19) for *Lumbricus*, a still higher degree of development has been attained, and a still higher degree of independence of the alimentary canal. A reminiscence of an earlier anatomical condition is however still retained, in the close connection of the dorsal vessel with the intestinal wall; thus FUCHS: “Das Gefäß (Vas dorsale) verläuft mediodorsalwärts über dem Darm, diesem eng angeschmiegt, mit Ausnahme der Pericordalregion. . . . Sowohl das Vas dorsale auf ganzer Länge besonders seitlich als diese Dorsointestinalia sind mit Chloragogen bedeckt.”

The species which is studied as a type of Oligochæta in the colleges of Northern India, and also at Calcutta, is *Pheretima posthuma*; and this being the form with which I am most familiar, it will be convenient here to describe shortly the vessels

in close connection with the alimentary tract, since these illustrate the increasing differentiation of the vascular system, and will be again referred to in the next section. I omit the ventral vessel, which is quite separate from the intestine, the parietal and subneural vessels, the hearts, the anterior loops, and the nephridial plexuses.

In *Pheretima posthuma* the dorsal vessel lies on the intestine, attached loosely to it in each segment by two pairs of vessels to the intestinal wall; these vessels join with corresponding branches from the suprainestinal and then pass transversely outwards on the intestine. The dorsal vessel is not covered by chloragogen cells; it becomes quite free anteriorly about segment x., and runs forwards at some distance above the alimentary canal, piercing the septa in succession, giving branches to the body-wall, and ending in front by disappearing into the wall of the pharynx at the level of the cerebral ganglion.

The suprainestinal vessel is distinguishable anteriorly about segment x. as a mid-dorsal channel in the alimentary wall; it extends back along the œsophagus and intestine beneath the dorsal vessel, communicating with the hearts in segments xii. and xiii., and with the alimentary plexus throughout its extent.

A subintestinal channel can be distinguished in the mid-ventral line on the anterior part of the intestine; it ends in front by dividing into a pair of ventro-lateral vessels in segment xiv., and posteriorly becomes indistinguishable behind the level of the intestinal cæca (segment xxvi.); it is a portion of the intestinal plexus, and hardly deserves a separate name.

The intestinal plexus consists of (1) transverse vessels, two pairs per segment, each formed by the union of a branch from the dorsal with one from the suprainestinal vessel; (2) close-set longitudinal channels, given off from the above transverse vessels, connecting successive transverse vessels with each other, and forming the main portion of the plexus; (3) oblique vessels, which, beginning near the mid-ventral line, incline forwards and dorsalwards, and pass through about three segments before reaching the mid-dorsal line, where they join the suprainestinal; (4) on the intestinal cæca are a number of longitudinal channels, meeting at the tip of the cæca, and connected in their course by numerous transverse vessels; (5) along the lateral aspects of the anterior portion of the intestine, from segments xiv. xxvi., are a pair of well-marked vessels, which, beginning ventrally in the alimentary plexus, incline gradually dorsalwards as they proceed backwards, and join the dorsal vessel at the level of the anterior margin of the intestinal cæca; (6) in segments xi.-xiv. (and therefore in front of the intestine) there are in the œsophageal wall a series of very definite and striking transverse vessels, about twelve pairs per segment, joining the suprainestinal above; the breadth of the vessels is at least equal to the intervals between them.

The postero-anterior contractility of the alimentary canal, which is so marked a phenomenon in the lower forms, begins to disappear, as has been shown, in the Tubificidæ; it has not, so far as I know, been described at all in the Megadrili. It has not, in them, been retained in connection with the intake of fluid by the anus, since

these animals do not live in a fluid medium; and it has not been retained for circulatory purposes, since a special propulsive mechanism, the dorsal vessel, has been differentiated.

We thus reach the end term of our present series. The anatomical development and differentiation of the vascular system have attained their maximum; and a completely separate dorsal vessel has taken over the function of propelling the blood, which in earlier stages was effected by the antiperistaltic contractions of the alimentary wall.

3. THE EVOLUTION OF THE VASCULAR SYSTEM IN THE ANNELIDA.

The short summaries which have been appended to the accounts of the several families treated of in the foregoing section have already made evident the general idea which the recital of the series is intended to convey; that is, that in the lower Oligochaeta the vascular system is, in its simplest form, intimately connected with the alimentary tube, largely as a series of vacuole-like intercommunicating spaces in the intestinal wall, in which spaces the movement of the contained fluid is determined by the antiperistaltic contractions of the wall of the tube; that in the higher stages of its development it comes to show, anatomically and physiologically, a large degree of independence of the alimentary tract; and that there are a number of intermediate stages which connect the simpler with the more highly differentiated condition.

It will not, of course, be supposed that the series of forms described in the preceding section is a linear series which reflects with exactitude the actual evolution of the vascular system of the Annelida. It seems, nevertheless, to be capable of affording a number of indications, and accordingly it may be useful to supplement the statement of the general proposition enunciated above by sketching, in the light of the foregoing observations, the possible course of evolution of some of the component parts of the system.

The Intestinal Network.

In the *Æolosomatidæ* the intestinal network is, in bulk as well as in physiological importance, the chief portion of the vascular system, and other vessels are few in number; the condition is not very different in the *Enchytraidæ*. In the higher groups it loses its preponderance, owing to the greatly increased development of peripherally situated trunks and capillaries.

I propose to regard the network as the primary constituent of the vascular system, and I believe that a recognition of its importance is a first requisite for an understanding of the evolution of the latter. In this connection I may quote VEJDovsky (54): "Das Magendarm-Gefässnetz ist überhaupt als Hauptbestandtheil des Gefässsystems der Oligochaeten zu betrachten"; and in a more recent communication (55) the same author speaks of the intestinal sinus as the most primitive portion of the vascular system.

The intestinal network is throughout the Oligochaeta situated within the muscular coat of the intestine; it will suffice to refer to the evidence collected by LANG (29,

pp. 210-218), and to VEEDOVSKY (55). The network will therefore originally be contractile, as, for example, it is seen to be in *Æolosoma*, since the muscular coat within which it lies is continually engaged in antiperistaltic action.

The further history of the intestinal network is the history of the differentiation from it of numerous vessels, which either separate completely or remain as specialised channels in the intestinal wall, and of the concomitant reduction in size and physiological importance of the network itself.

The Dorsal Vessel.

Since the antiperistaltic movements of the whole gut-wall necessitate a forward movement of the fluid contained in the irregular system of intercommunicating spaces in the wall, the specialisation of definite channels may be expected to follow. The dorsal vessel is one of such; and it is the one in which contractility, originally the contractility of the gut-wall, becomes specially developed.

In the Enchytræidæ there is, in the greater part of the extent of the body, no differentiated dorsal vessel at all. In *Æolosoma hemprichi* a small mid-dorsal channel is differentiated in the plexus on the stomach, but not on the intestine; in *A. viride* this channel may extend back on to the anterior part of the intestine. In the Naididæ the dorsal vessel is distinct throughout the body, incorporated in the alimentary wall along the whole of the intestine. In the Tubificidæ it is in general in close contact with the intestinal wall, and is surrounded by chloragogen cells; in *Branchiura sowerbyi*, however, it does not lie immediately on the intestine, but has, nevertheless, a closer relation to the gut and chloragogen cells than has the ventral vessel. The relations in the Tubificidæ are repeated in the earthworms (*Lumbricus* and *Pheretima*).

But if the intestinal part of the dorsal vessel is thus a specialisation of the alimentary network, its remaining portion will hardly own a different origin. An indication that the œsophageal portion of the vessel arose in a similar way is to be seen in the cellular strands which pass across the lumen of the "heart" of *Æolosoma hemprichi*; these may represent, as has already been suggested, vestiges of the partitions of an original lacunar system, which at an earlier stage invested the anterior as well as the posterior portion of the alimentary tract.

The differentiation of the circulatory system, as of the alimentary tube itself, has thus proceeded further in the anterior part of the body than in the posterior. The principle holds throughout; it is seen in the ventral vessel of *Æolosoma* as well as in the dorsal; it is seen in the relations of gut-plexus and dorsal vessel in the Enchytræidæ; it is seen also in the fact that in most aquatic Oligochaeta the dorsal vessel, while incorporated in the alimentary wall in the intestinal region, runs free in the coelom anteriorly; while in the earthworms also the anatomical separation of the dorsal vessel from the alimentary canal is much greater in the œsophageal region than over the intestine.

The Ventral Vessel.

In *Æolosoma hemprichi* the ventral vessel appears in the anterior part of the body as a distinct vessel in close anatomical relation to the alimentary canal; in the intestinal region it is represented by a median ventral sinus-like channel on the intestinal wall, which loses itself behind in the vacuolar spaces of the alimentary network. In all the other groups of Oligochaeta described above the ventral vessel is an independent vessel in its whole length, separate from the alimentary canal, and connected with the alimentary network by a number of mesially situated short communicating channels.

The Ventral Vessel an Earlier Differentiation than the Dorsal.—The ventral vessel thus shows throughout the series a higher grade of differentiation than the dorsal vessel. In *Æolosoma*, the lowest term of the series, it has attained a degree of development approximately comparable to that which the dorsal vessel shows in the Naididae. In the higher terms of the series its greater anatomical separation from the alimentary canal, and its freedom from chloragogen cells, show that it is still ahead, and so to speak maintaining its lead. It may be mentioned that embryologically also the ventral vessel begins to be developed before the dorsal.

The above considerations render it allowable to suppose that, as the dorsal vessel has been differentiated from the alimentary plexus, so also, but at an earlier stage, has the ventral. While the earlier stages in the evolution of the dorsal vessel are exemplified for us in the lowest terms of our anatomical series, the final in the later; and while the evolution of the suprainestinal and subintestinal trunks has not yet begun in the lower forms, though it has made considerable progress in the higher; the ventral vessel, on the other hand, began its evolution at a phylogenetic stage of which representatives are no longer extant. Hence it is only the later portion of the evolution of the ventral vessel that is actually exemplified in our available material.

In another way, and even more markedly, the ventral vessel is distinguished from the dorsal. The dorsal vessel, both in its earlier form as a channel in the intestinal wall, and again after its separation from the gut, maintains its contractility; the ventral vessel is from its first appearance non-contractile. We may ask, therefore—(1) Why should the ventral vessel be the first to be differentiated? and (2) why, even while still attached to the intestine (*Æolosoma*), should it lose its contractility?

The answer must be as follows:—The effect of the antiperistaltic contractions of the intestine must be to drive the fluid contained in the network in a forward direction, and, in a closed system, a channel must necessarily exist by which the fluid can return; the ventral vessel is such a return channel. Again, this channel must, to fulfil its purpose, be from its first appearance to some extent at least outside the influence of these contractions. If under these circumstances the ventral vessel were to be contractile, the contractions would have to be antero-posterior; but this is impossible, since vascular contractility is a derivative of that of the intestine, which is postero-

anterior. The best that can happen, therefore, is that the ventral vessel should simply lose its original contractility altogether.

This it does; muscle cells are indeed abundantly present, as has been shown, among others, by VEJDovsky (55), SCHNEIDER (42), and STERLING (52), for both lower and higher forms; but, although isolated statements to the contrary have been made, it will be admitted that the ventral vessel is in general non-contractile throughout the group.*

The Earliest Differentiations are in the Middle Line. — Can we assign any reason why the specialised longitudinal tracts in the intestinal network, which come to form the dorsal and ventral vessels, should appear in the median line?

The lateral bending movements of a worm-like animal must cause temporary obliteration of the spaces on the sides of the alimentary tube on the convexity of the curve by the stretching out of the wall, and on the concavity by the squeezing together of the wall in which the spaces lie. The only regions unaffected by these deformations are the mid-dorsal and mid-ventral lines; hence along these lines clear channels for the flow of fluid might be formed, which would not be impeded in consequence of lateral flexions of the animal's body.

It is, of course, the case that the chief vessels in Nemertines are laterally situated; but they are not in the same close connection with the alimentary canal as in the forms now under consideration, and it is at least possible that the vascular system did not arise in the same way in that group.

The Supraintestinal Vessel.

The supraintestinal vessel is a differentiated portion of the alimentary network which exists only in certain of the anterior (œsophageal) segments of the body in the

* BEDDARD (3) states that the ventral vessel is contractile in *Phroryctes*. HARRINGTON (*apud* LANG, 29) makes the same statement with regard to earthworms, though the pulsations "are never so well marked as in the dorsal" vessel. SCHNEIDER (42), in saying "Somit sind beim Regenwurm alle Gefässe mit Ausnahme der kleineren Venen und der Kapillaren kontraktile," is apparently arguing merely from the presence of muscular fibrils, and therefore begs the question. STERLING (52), while admitting the ventral vessel in earthworms to be "sehr wenig kontraktile," adds "auch das Studium ganz junger durchsichtiger Embryonen erlaubte mir nicht, die Kontraktilität deutlich zu beobachten." FUCHS (19, p. 477) does not allow the ventral vessel among those portions of the vascular system of Annelids that may show contractility; he states, however (*ibid.*, p. 460), that according to CLAPARÈDE it is contractile in *Haplotaxis*, and adds, "Das ist die einzige mir bekannt gewordene positive Angabe von einem kontraktilem Vas ventrale." VEJDovsky (55) takes up the same position as SCHNEIDER; thus (*loc. cit.*, p. 140) he says, "Dass die Intestinalgefässe gewiss kontraktile sind beweist ihre muskulöse Umhüllung, namentlich der in das Rückengefäss ausmündende Abschnitt"; and again (*loc. cit.*, p. 157), in a statement which includes the ventral vessel, which is our present concern, "Sämtliche Bestandteile des Gefässsystems sind mit Muskelfasern versehen, und somit müssen alle kontraktile sein, mag man sie auch als nicht kontraktile bezeichnen." The argument seems to me to be defective, and much as if one should argue that a man must be able to move his ears because he possesses a series of muscles attached thereto. VEJDovsky expresses himself more cautiously in another place (*loc. cit.*, p. 147), where he says, "Es sind also dem Baue nach alle Gefässe kontraktile, oder besser, alle bestehen aus Muskelzellen."

Taking the last statement as correct, is it not possible to apply the principle of change of function? The vascular system is developing, throwing out extensions; the material at hand for building it is muscle cells. These are not required to be contractile throughout; hence, though still recognisable as muscle cells, they become, in certain parts of the system, merely passive building materials. They may even lose their distinctive histological characters; cf. VEJDovsky, in a sentence which occurs immediately before the one last quoted, "Schliesslich sind die Zellen, aus welchen die feinsten Capillaren bestehen, in die Kategorie der Muskelzellen zu stellen, wenn auch hier keine fibrilläre Struktur nachweisbar ist."

At any rate, the question of contractility is rather one for actual observation than for decision by inference from histological structure.

Tubificidæ; in *Pheretima* it extends backwards along the intestine also. It is, however, by no means invariably present in the higher Oligochaeta (*cf.* the data given by FUCHS, 19).

In the Tubificidæ BEDDARD (3, p. 69) considers that this vessel is in the anterior part of the body the homologue of the dorsal vessel in the posterior part, and that the anterior part of the dorsal vessel, which occurs along with and above the suprainestinal in the œsophageal region, is a new structure. But it is to be noted that even in the Naididæ the anterior part of the dorsal vessel is less intimately related to the alimentary canal than the posterior; and that in *Pheretima* (and *Pontodrilus*, *cf.* FUCHS, *loc. cit.*) the suprainestinal is not confined to the anterior part of the body, but extends the whole length of the intestine.

A more acceptable view of the relations of the suprainestinal would seem to be the following:—With the progressive differentiation of the vascular system the dorsal vessel separates itself from the intestine; such differentiation proceeds, as we have seen, more rapidly in the anterior than in the posterior part of the body; the same causes which led to the specialisation of the dorsal vessel as a median channel in the intestinal network again become active after the separation of the dorsal vessel from the intestine; and hence we have the formation of the suprainestinal, at first in the œsophageal region, and later, when the dorsal vessel has attained a considerable anatomical separation along its whole length (e.g. *Pheretima*), throughout the entire extent of the intestine.

The Subintestinal Vessel.

The subintestinal vessel is well known in certain Tubificidæ, where it corresponds in position on the ventral side of the œsophagus to the suprainestinal on the dorsal side. It is not recognised by FUCHS as occurring in any of the higher groups. If, however, reference be made to the account previously given of the blood-vessels in connection with the alimentary canal in *Pheretima posthuma*, it will be seen that there is in that species a channel on the anterior part of the intestine to which the name may be applied. A similar mid-ventral channel occurs on the “crop” in *Chaetogaster orientalis* (*vide ante*); according to FUCHS (*loc. cit.*, p. 454) the same vessel has been described in *Chaetogaster crystallinus* by LEYDIG, and in *Lumbriculus* by BÜLOW. The subintestinal may therefore be looked on as a specialisation of the alimentary network showing various degrees of development, and formed after the separation of the ventral vessel in the same way as the suprainestinal after the separation of the dorsal.

Other Specialisations of the Alimentary Network.

These are sufficiently illustrated by the foregoing description of the intestinal network of *Pheretima*, which, belonging to the Megascoleidæ, may be looked on as one of the most highly developed forms of the Order. The transverse channels of the

plexus, on both intestine and œsophagus, are the most obvious; but the system comprises numerous and definite longitudinal and oblique vessels also.

We thus have anatomical evidence that a very considerable proportion of the blood-vessels in both lower and higher Oligochæta are derived from the alimentary plexus, which, situated in the gut-wall, is the most primitive portion of the system; the vessels have arisen by a progressive differentiation of the channels in the plexus, which at first, as still in *Eolosoma*, consisted of a system of irregular lacunar spaces.

Of the remaining portion of the vascular system, I propose to consider in detail only the lateral loops or commissures, a certain number or all of which are, like the dorsal vessel, contractile, and share in the function of propelling the blood.

The Lateral Commissures.

The direct evidence for the origin of the lateral loops from the alimentary network is less than in the case of the vessels previously considered, and the earlier stages of their development are not clearly documented for us. The argument must be largely one of analogy.

The contractility of the dorsal vessel is originally the same thing as the contractility of the gut-wall; and unless we are to assume an altogether different origin for the contractility of the commissures, these also must be imagined as having their origin in the gut-wall and as having later separated from it.

Anatomically, it is perhaps worth while to recall such features as the parallel channels running transversely between dorsal and subintestinal vessels in the crop of *Chatogaster*, and the well-marked transverse vessels in the intestine and œsophagus of *Pheretima* and other earthworms. These examples show that not only longitudinal, but transverse channels also, may be formed in the gut-wall. From such channels the commissures may be supposed to have arisen, separating themselves from the alimentary wall in a manner like that of the dorsal and ventral vessels. As to why such channels only separate from and become independent of the alimentary canal to the number of one pair per segment, the answer is probably that this can only happen where there is some support for them, along which they can travel, *i.e.* can only happen at the positions of the septa.

Is a Small or a Large Number of Commissures the Primitive Condition?—In the Tubificidæ and in the higher families of the Oligochæta there is, speaking generally, a pair of lateral loops to each segment of the body; in *Eolosoma* there are none, in the Naididæ and Enchytraeidæ a few only, situated in the anterior region. Which condition are we to look on as primitive? In other words, are we to consider the small number of loops in the Naididæ and Enchytraeidæ as the remnant of an originally complete series, and is *Eolosoma* the last stage in the path of degeneration?

Let us consider first the case for degeneration. It has, in fact, been urged by BEDDARD (3, pp. 72, 167, 170) that *Eolosoma* and the Naididæ, though simple forms, are secondarily simple, and not primitively so.

(1) Anatomical evidence in support of this position is not wanting in the case of *Eolosoma*; the cerebral ganglion remains attached to the superficial epithelium throughout life, and the ventral nerve cord is absent, or, at any rate, only demonstrable with difficulty as a rudiment. Again VEJDovsky (54) found in occasional specimens of *A. ehrenbergii* (= *hemprichi*) two fine lateral commissures given off from the pharyngeal vascular ring, which he thought joined the dorsal vessel; these might be looked on as vestiges of lateral loops which in most individuals have entirely disappeared. As regards the Naididæ, however, apart from certain peculiarities in the genus *Chatogaster*, which I have previously argued is descended from parasitic ancestors, I cannot recall any features in the adult anatomy which point clearly to degeneration. The same may be said of the Enchytræidæ, which, like the Naididæ, have only a small number of lateral commissures.

The answer to the argument for the degeneracy of the lower families of the Oligochæta would be that admitting it as probable for *Eolosoma*, at least as regards certain features, still degeneration in respect of certain structures does not mean degeneration in respect of all; that BEDDARD himself (3) derives *Eolosoma* from the base of the Oligochæte stock; and that in any case degeneration has not been made out for the Naididæ and Enchytræidæ. At the same time VEJDovsky's observations quoted above carry weight as regards the decision of the question in *Eolosoma*.

(2) The prevalence of asexual reproduction in *Eolosoma* and the Naididæ may be used as an argument for their degeneracy. Thus BEDDARD (3, p. 170), for *Eolosoma*, adduces the statement of MEYER, that asexual reproduction only occurs in undoubtedly degenerate forms, or in those forms where sexual products abound in the posterior as well as the anterior part of the body. But MEYER's position is, I think, difficult to substantiate, and the statement is probably too sweeping; and to use it in support of the present contention is to take for granted the precise point at issue. Moreover, the argument does not touch the Enchytræidæ.

(3) BEDDARD (3) quotes BOURNE's observations (8) on *Uncinaxis littoralis*, in which species a regular series of loops was found to be present in the budding zone of those individuals which were reproducing by fission. BEDDARD, using the word "bud" apparently in the sense of a young individual, states (from BOURNE) that "in the young buds commissural vessels occur in all the segments" (*loc. cit.*, p. 295; *cf.* also pp. 72, 277, in the same sense), most of which vessels afterwards disappear. It is inferred that phylogenetically, also, the Naididæ as a family primitively possessed an extensive series of loops reaching to the posterior end of the body, and that these have secondarily become reduced in number.

It is necessary, in order exactly to understand the position, to refer to BOURNE's original description, and especially to his figures. We have not a complete account of the history of these loops; but what BOURNE states, and what his figure shows, is that the loops are present in the actively growing regions of the worm, *i.e.* the zone of budding and the posterior end of the animal. It is, however, clear that no individual

of a chain ever has a *complete* series of loops; and that of the loops which are actually formed, a certain number at least do not disappear, but persist, in an adult worm, in the middle of the animal's body; this is shown by BOURNE's fig. ii., since the loops of the segments numbered xviii., xix., xx., xxi., in that figure belonged, before the onset of asexual reproduction, to segments xviii.–xxi. of the parent animal, and were not produced in a budding zone.

An opponent might therefore reply that if the above interpretation of BEDDARD is correct (in supposing that he bases his position on the appearance of a complete series of loops, most of which subsequently disappear), it would seem that his argument needs modification; that it is doubtful how far the processes of asexual reproduction are significant in a consideration of phylogeny; and lastly, that while the interest and importance of the observations are admitted, it will be advisable to wait for a complete account of the history of the loops before drawing conclusions, and before extending them to the Naididæ in general and especially to the Euehytræidæ and Æolosomatidæ.

(4) However the case may stand with regard to *Uncinatis*, we have in *Branchiodrilus* a genus of Naididæ in which a complete series of lateral loops exists in the adult condition. It may be argued that here at least there is exemplified for us the primitive condition, in comparison with which the remaining genera are regressive.

The question then is, Is a single form, *Branchiodrilus*, to be looked on as progressive as compared with the rest of the Naididæ; or are these to be looked on as degenerate in comparison with *Branchiodrilus*?

Branchiodrilus is a specialised form; the loops are throughout a considerable portion of the body continued into the gills; and it is thus the presence of an extended series of lateral loops which gives the possibility of the development of the gills, which they supply with blood.

It is open to us to suppose, therefore (*a*) that a progressive variation, viz. the production of an extended series of loops, has been seized and taken advantage of for the development of gills; (*b*) or, considering the complete series of loops in *Branchiodrilus* to be a primitive feature, that the development of gills is the reason of the retention, in this isolated case, of the lateral loops which have disappeared in the other genera.

The first alternative would appear to be preferable, since the loops extend throughout the body, including the posterior region, whereas gills are absent from the hinder part of the animal.

The argument is not conclusive either way; but it appears to tell rather against than for the assumption of a complete series of loops as a primitive condition.

The opposite side of the question, *i.e.* that a small number of loops situated in the anterior part of the body represents the more primitive condition, the complete series being a later development, may now be considered.

(1) In the first place, there is the fact that the circulatory system as a whole does broadly, as has been shown, exhibit a gradual advance from the condition in *Æolosoma*

through the Enchytræidæ, Naididæ, and Tubificidæ, to that presented in the higher families of the Order. Again, speaking broadly, it is scarcely feasible to read this series downwards, as a number of successive stages in a process of degeneration; it would, for example, be difficult to suppose that a developed dorsal vessel has united with the gut-wall and finally dissolved in the vascular network; and it would be impossible to contend that the contractions of an originally distinct dorsal vessel, which were by chance in the same direction and of the same nature as those of the underlying intestine, united by a series of stages with those of the gut in proportion as these structures became gradually united anatomically, until finally there was a physiological fusion and solution, if I may use these terms, similar to the anatomical fusion and solution.

It may, of course, be urged that the lateral loops might nevertheless undergo degeneration while the rest of the system continued on the upward path. But it is unlikely that in a system which has been shown to be generally progressive so important a part should develop in a contrary direction, and the burden of proof must lie on those who suggest it.

(2) The fact that there are a certain number only of lateral loops, and these in the anterior part of the body, in the Naididæ and Enchytræidæ, is in harmony with the idea of a progressive rather than a regressive development. We have seen that the anterior region is the region of greatest differentiation of the vascular as of the associated alimentary system; the dorsal vessel first appears here as a distinct vessel; when formed throughout the length of the body, it separates from the alimentary canal here first; an indication that the ventral vessel develops in a similar way is seen in *Eolosoma*; the suprainestinal and subintestinal vessels are developed first, or only, in the anterior region; and as regards the transverse channels, it may be recalled that in *Chatogaster* the parallel transverse vessels in the alimentary wall are most regular, numerous and conspicuous on the crop, less so on the stomach, and become indistinguishable on the intestine. We should, I think, naturally expect to find the separated lateral commissures at first few and anterior, as in *Nais*, *Pristina*, *Dero*, etc.; then more numerous and extending further back; and finally in regular series throughout the body, as in *Branchiodrilus* among the Naididæ, in the Tubificidæ, and in the earthworms.

It appears to me, however, to be impossible at present to come to a definite decision on the question; and accordingly the above statement of the arguments on both sides is all that will be attempted here.

The Course of the Circulation.

The relations between the contractions of the alimentary wall and those of the dorsal vessel, previously described, explain to us the fact that the course of the blood in the dorsal vessel of the Annelida is from behind forwards. Even where this vessel

is no longer in direct association with the intestine it still retains, in the direction of its contractions, a mark of its origin.

The course of the blood between intestinal network and dorsal vessel has been variously stated. Thus BEDDARD (3, p. 74) states that in the Naidomorpha and Tubificidæ "the (intestinal) network is fed from the dorsal vessel, and the blood returns into the ventral vessel"; adding, "the network at any rate has connections with both vessels" (this is denied, however, on p. 240 as regards the connection of the network with the ventral vessel in the Tubificidæ, except *Ilyodrilus*). VEJDovsky, on the other hand (54, p. 115), speaking of the Oligochaeta in general, says: "There are usually one or two pairs of such thicker anastomoses (between intestinal network and dorsal vessel) in each segment, which conduct the blood from the network to the dorsal vessel"; and (p. 113) the dorsal vessel "is to be regarded as the organ for the collection and propulsion of the blood which enters it from the intestinal network of vessels." BOURNE also thought that the blood went from the intestine to the dorsal vessel and not *vice versa* (cf. BEDDARD, *loc. cit.*, p. 76).

In the absence of floating corpuscles in the blood, actual observation of the direction of the flow is difficult. VEJDovsky's view is however the one which harmonises better with the considerations here put forward. The fluid in the network is moved forwards by the antiperistaltic contractions of the intestinal walls; and since the specialised median dorsal channel is first developed as a forward continuation of the path taken by the fluid, which travels in the same direction in both, the fluid must enter the dorsal vessel from the network, and not *vice versa*; the ventral vessel, having been specialised and early separated from the intestine for the purpose of providing a return channel, must deliver the blood again to the network.

The Origin of the Vascular System.

In the present section I have attempted to sketch the evolution of the various components of the vascular system of the Oligochaeta, the idea on which the sketch is based being that that evolution has proceeded by progressive differentiation of the intestinal plexus, with the formation and separation from the intestinal wall of distinct blood-vessels. Such an evolution has been clearly traced for the dorsal, suprainestinal, and subintestinal vessels; and there are at least indications of a similar origin for the ventral vessel and the lateral commissures. We come then to the conception of a simple series of intercommunicating vacuole-like spaces in the wall of the alimentary canal throughout its extent, as the first representative of the circulatory system. The final question is, How did these fluid-containing spaces originate?

The suggestion that most readily presents itself is that the spaces originated by transudation of liquids from the lumen of the gut; in using the word "transudation," however, it is not intended to exclude an active participation of the intestinal epithelium in the process. The alimentary matters introduced by the mouth, it is to be supposed,

passed, after being reduced to solution, through the epithelial wall; similarly a certain amount of water carrying oxygen and dissolved matters, introduced at the anus. These fluids tended to accumulate in a series of spaces which they made for themselves external to the alimentary epithelium; as the spaces increased in size, they became confluent; and thus was established the alimentary network, from which by progressive differentiation the vascular system was later evolved.

4. THE THEORIES OF LANG AND VEJDOVSKY.

The foregoing considerations are based on observations on one order only—that of the Oligochaeta, and of certain families only within that order. Though these considerations apparently help to explain the origin of the vascular system in the group on which the observations have been made, it is quite possible that the explanation may not be of universal application; it will, however, in all likelihood be found applicable to the Annelida in general, and consequently to any groups which can be shown to be descended from these. But it appears possible that the vascular system is not homologous throughout the animal kingdom, and that in the Nemertines, for example, it may own a different origin.

The observations also, while partly anatomical, are largely from the side of physiology. I have not, however, attempted to emulate the painstaking histological researches which have of late been directed, by a number of observers, towards the elucidation of the problem here considered. But such agreements as are found between the results here attained, and those reached by other workers, on other groups and along other lines, will be of value from the very fact that the path here pursued has been a different one.

The first agreement that I have in mind is that which exists between the results here reached and those put forward by LANG (29), in respect of the same question. LANG's theory, based on anatomical and also especially on histological evidence, collected in great quantity and detail, and discussed in the work just referred to, supposes the vascular system to have had its origin in the diffusion of fluid into the space between the epithelium of the alimentary tube and the surrounding mesoblastic elements, which, in accordance with the gonocoel theory of the origin of the coelom, are conceived as genital pouches. At its first appearance the system is thus constituted by a perienteric sinus, with ring-like centrifugal extensions between the transversely placed walls of successive gonadial chambers, and dorsal and ventral extensions in the sagittal plane (mesenterial sinuses) between the adjacent inner walls of the right and left chambers of the same pairs. The main blood-vessels, dorsal, ventral and lateral commissural, are specialisations of this common reservoir, determined as to their position by the places in which the neighbouring walls of the coelomic (gonadial) chambers come together and fuse. The similarity, in a general way, of the view put forward in the last section with the central idea of LANG's theory needs no emphasis.

LANG sets forth his conclusions in the form of a number of theses (pp. 192-200); of these, those which more particularly agree with the views put forward above are the following:—

(1) (Theses 2, 3).—Though, as will be seen below, the matter of these two propositions is not completely in accord with my views, one idea contained therein finds expression also in the present paper: viz. that the blood-vascular system originates in the diffusion of fluid from within the intestinal cavity into a space (or series of spaces) outside the epithelial layer.

(2) (Thesis 11).—Here is expressed the view that the first vessel which separated from the perienteric sinus, and so became independent, was the ventral vessel; and that thus the return of the blood, which travels forwards in the sinus, was provided for.

(3) (Thesis 28).—The musculature of the longitudinal vessels is here derived from the musculature of the intestinal wall; at first, before the complete separation of these vessels from the sinus (I should prefer the word “plexus” where the reference is to the primitive condition), the muscular coat would be wanting above (in the case of the ventral) or below (in the case of the dorsal vessel); a complete investment would be attained when the vessels had become fully separated. This agrees with the physiological observations which I have recorded above, and describes the manner in which the anatomical differentiation, which corresponds to the physiological differentiation of two separate contractile rhythms, must have taken place.

If in what follows I dwell at greater length on certain of the differences between LANG's conception of the early history of the vascular system and my own, it will be understood that this is not because the importance of the differences outweighs the essential agreement, but because of the necessity I am under of justifying, to the extent of my ability, my temerity in opposing myself to so distinguished an author and investigator.

(1) (Theses 2, 3).—LANG, deriving the earliest Annelids from Turbellarian-like forms with metamerically branching alimentary space and numerous gonadal sacs occupying the intervals between the neighbouring branches, supposes that these sacs swelled to form a chambered coelom; that in proportion as this took place the interposed branches of the alimentary cavity shortened and disappeared, leaving a space in their stead; which, becoming filled with nutritive fluid diffusing through from the intestinal cavity, formed the origin of the vascular system. At first this consisted of a (continuous, *vide* LANG's fig. 2) peri-intestinal sinus with, as prolongations therefrom, septal and mesenterial sinuses between adjacent chambers of the coelom.

On this I may perhaps remark, that if the branches of the alimentary cavity shrank only in proportion as the gonadal sacs swelled (in dem Masse, als sich die Sackgonaden zu Gonocölsäcken erweiterten), no space would be left. If such were left, it would not represent a peri-intestinal sinus (since nothing is said as to the shrinking of the main intestinal tube), but a series of septal sinuses. And lastly, my main point is that the transudation of fluid, when the latter first began to accumulate between intestinal

epithelium and gonocœl wall, would presumably at first give rise to a number of vacuole-like spaces; later, these would spread and fuse here and there to form a network; while in some cases the process might go further still, and result in the formation of a peri-intestinal sinus. My own idea of the formation of a sinus, in those cases where it occurs, corresponds to the description by GAMBLE and ASHWORTH (20) (also referred to by LANG, p. 210), who show that the intestinal sinus in the Arenicolidæ is a secondary formation; the original condition ontogenetically is that of a plexus, which later gradually extends itself by the fusion of the individual vessels to form a continuous sinus. I cannot help thinking that LANG has added to the difficulties of the theory by assuming a continuous sinus as the original condition, from which, in most cases, a network has been formed by subsequent approximation and adhesion of the tissues of the cœlomic wall to the alimentary epithelium.

The evidence, I think, is the other way. Firstly, as stated above, it seems on mechanical grounds easier to conceive the network as giving place to the sinus than *vice versâ*. Secondly, the network is the commoner, the sinus the rarer condition; and, indeed, this is probably the case in greater degree than at first sight appears, since what is really a network has frequently been called a sinus.* And thirdly, as mentioned above, in the Arenicolidæ a plexus does actually give place to a sinus during individual development.

(2) (Thesis 9).—The contractility of the vascular walls is supposed by LANG to be derived from the contractility of the walls of the gonadial sacs, which came into play primarily for the purpose of expulsion of the genital products; these contractions

* We may take, for example, the case of the Enchytræidæ (*cf.* LANG, *op. cit.*, pp. 210–216). The perienteric “sinus” here, according to MICHAELSEN (quoted by LANG), is “eher ein dichtes Netz von Blutkanälen,” or, according to another paper of the same author, “besteht aus vielen hart nebeneinander verlaufenden Kanälen.” So, too, I have observed in a specimen of *Lumbricillus subterraneus*, in which the posterior part of the body was much engorged and the blood coagulating, that the appearance in the alimentary wall was that of a thick, close-set network of large vessels, with hardly any interspaces between them.

BEDDARD, discussing this point (quoted by LANG, p. 215), also speaks of a network, and doubts the existence of a continuous sinus. LANG here takes BEDDARD to task, remarking, “Sodann bezweifelt BEDDARD auch, man weiss nicht weshalb, die Richtigkeit der verschiedenen Angaben von MICHAELSEN und VEJDovsky über den Darmblutsinus der Enchytraiden.” LANG is, however, wrong, at any rate as regards BEDDARD’s attitude towards MICHAELSEN. MICHAELSEN speaks of “a close network of blood-channels,” and of “numerous closely approximated channels.” Though such a condition may perhaps loosely be called a “sinus,” it is certainly more properly described as a network; BEDDARD, using the words in their strict significance, is in agreement with MICHAELSEN’s facts, though possibly differing in the name he uses to denote the condition.

As illustrating the loose use of the term “sinus” referred to in the text, I may take two instances, quoted by LANG though with a different object. On p. 214 HESSE is apparently made to speak of “Darmsinuskanäle,” and “Darmsinus-kapillaren”; and LANG himself a few lines lower speaks of “die Kanäle des Blutsinus”; such expressions are, to my thinking, self-contradictory, since, if a system consists of canals or capillaries, it cannot at the same time be a continuous space,—which is what I take the word “sinus” to mean, and which is the sense required by LANG throughout his discussion of the origin of the vascular system. Again (top of p. 217), HESSE speaks first of a “blood-sinus,” then of cells whose long diameter coincides with the axis of the “blood-vessel” (des Blutgefässes), and lastly of a “blood-sinus” again. I may add that VEJDovsky apparently uses the expressions “sinus” and “network” without distinction; thus (55, p. 155, 156), “sog. Darmblutsinus” and “sog. Blutsinus,” of Oligochaeta in general; (p. 85) of *Pheretima*, “des sog. Blutgefässnetzes (Darmblutsinns)”; (p. 119) “Darmsinus” and “Darmblutsinus,” of *Pheretima*; (pp. 125 and 139) “Darmblutsinus,” of *Dendrobana*, a Lumbricid; it would seem that he holds the view that the system is essentially a sinus throughout the Oligochaeta:—“Der Darmblutsinus (of *Pheretima*) gestaltet sich von der Oberfläche als das sog. Darmgefässnetz, indem er in einzelne längs- und ringsverlaufende Kanäle abgeteilt ist, die untereinander kommunizieren. An Querschnitten erscheint er als eine mächtige Lakune . . .” (p. 119).

became more and more subservient to the needs of the circulation ("Die Kontraktionen der Gonocölwände . . . konnten sich immer mehr und immer spezieller in den Dienst dieser Blutbewegung stellen").

As will be apparent from the foregoing, the contractility of the blood-vessels is to be derived from the antiperistaltic contractions of the gut (which had not at first a specially circulatory significance); and these are to be looked on as a primitive characteristic of the alimentary canal (*vide post*, p. 780).

(3) Thesis 20 runs as follows:—"Dass die Darmmuscularis ursprünglich dem Darmepithelrohr fremd ist, erhält eine interessante Illustration durch die vielfach beobachtete Tatsache, dass ihre Kontraktionswelle bei den mit einem Darmblutsinus ausgestatteten Polychäten antiperistaltisch verläuft. Sie dient hier nur als propulsorischer Apparat des vom Darmsinus in das Rückengefäß strömenden Blutes." The limitation (bei den mit einem Darmblutsinus ausgestatteten Polychäten) is needless; the contractions are antiperistaltic in the aquatic Oligochaeta, and also, as will be shown in the second part of the present paper, in a number of families of Polychæta which do not possess a perienteric sinus.

LANG apparently here bases himself on WIRÉN's statements with regard to the Polychæta (p. 206): "Die fast immer stattfindenden peristaltischen Bewegungen der Ringmuskulatur schreiten bekanntlich von hinten nach vorn fort. Sie haben also eine andere Aufgabe als die Nährstoffe zu bewegen"; but this purpose is not respiratory, for "der hauptsächliche und wahrscheinlich der einzige Zweck der peristaltischen Bewegungen ist, wenigstens bei denjenigen Anneliden, welche in der Darmwandung eine grosse, mit Blut ausgefüllte Lakune besitzen—und dies scheint wenigstens bei allen sedentären der Fall zu sein—das Blut der Darmwandung vorwärts zu treiben."

The statement which I here wish to oppose, which occurs in the quotations from both LANG and WIRÉN, is that the antiperistaltic contractions of the intestine in the Polychæta are altogether circulatory in their purpose, and not at all respiratory. In the first place, the antiperistaltic movements are associated apparently for a common purpose, and in Polychæta as well as in Oligochaeta (as a reference to the second part of this paper will show), with an ascending ciliary action, which can have no effect on the circulation. Secondly, the antiperistaltic contractions are usually much more violent than would be necessary for the movement of the fluid in the intestinal network, since they cause a considerable constriction of the alimentary tube and may even entirely occlude its lumen; they have therefore presumably some other function than the circulation to subserve, and this can hardly be other than the forward propulsion of matters in the alimentary canal, *i.e.* largely of fluid introduced at the anus, where the antiperistaltic contractions begin and are usually most violent. Thirdly, the combined effect of antiperistalsis and ascending ciliary action demonstrably is to introduce fluid into, and to propel it along, the alimentary canal (*cf.* also the observations on Polychæta in Part II., and especially pp. 804, 811, on the "gulping" action of the anus and the antiperistaltic waves which follow on this); the result must

necessarily be the absorption of oxygen (and dissolved food-matters) by the intestinal epithelium.

I cannot find that any evidence *against* the respiratory nature of the phenomenon is adduced; there would therefore seem to be no reason to doubt that the antiperistaltic contractions have at the present day the double function of moving in a forward direction both the blood in the network and the fluid in the alimentary canal.

(4) (Thesis 21).—"Die antiperistaltische Bewegung der Muskelwand des Darmblutsinus (der visceralen Muskelschicht der Gonocölsäcke), die sich in die von hinten nach vorn verlaufende Kontraktionswelle des Rückengefäßes fortpflanzt, welches selbst nur eine vordere mediodorsale Fortsetzung des Blutsinus ist, hatte vielleicht ursprünglich den Sinn, die im resorbierenden hinteren Abschnitt des Darmes gewonnene ernährende Flüssigkeit auch dem vorderen Körperteile zu gute kommen zu lassen. Das innere Flimmerkleid des Darmes besorgte allein die analwärts gerichtete Fortbewegung des Darminhaltes."

In Thesis 20 (*vide supra*) the statement was made that (in the Polychæta) the sole function of the antiperistaltic contractions is circulatory. Here it is stated that this is perhaps also their original function ("... hatte vielleicht ursprünglich den Sinn..."). This is, of course, opposed to the general argument of the present paper, according to which the antiperistaltic contractions are an original property of the alimentary canal subserving ingestion, and only secondarily brought into the service of the circulation.

In the first place, it will be agreed that peristalsis, in whichever direction it proceeds, has throughout the animal kingdom, speaking generally, the function of moving matters contained in the lumen of the tube, not in the substance of its wall.

In the second place, peristalsis (under which head I include for present purposes antiperistalsis) is known at lower levels in the animal kingdom than the Annelida. It occurs, for example, in the œsophageal tube of Actinozoa; thus CARLGREN (11) describes how ingestion is mainly accomplished by peristalsis in *Tealia*, *Actinostola*, and *Bolocera*, and is partly effected by the same means, with the help of ciliary action, in *Caryophyllia*; peristaltic action is also said possibly to assist in the expulsion of solid food-remains in *Tealia* and *Actinostola*. Again LANG (28) describes in Polyclad Turbellaria a series of sphincter-like bands of muscular tissue on the branches of the alimentary canal, which can contract so far as to obliterate the lumen; by means of peristaltic-like contractions of these bands the fluid contents of the main channel of the alimentary canal are driven throughout the system as far as the end branches, and afterwards back into the main tube again.

Arguing from the comparative standpoint, therefore, it would seem that the original function of peristaltic contractions in the animal kingdom was to move in one direction or other substances contained within a tube-like cavity.*

* It is perhaps rather disingenuous on my part to introduce the Polyclada as an example drawn from a lower phylogenetic level, seeing that I am doubtful about accepting LANG's theory of the derivation of Annelids from Turbellarian ancestors; I am not sure that there is not more truth in HUBRECHT's view, which is the reverse of LANG's. LANG, however, and those who think with him, will appreciate the force of the example in this connection, even if it does not appeal so strongly to me. In any case, there remains the fact that peristalsis occurs amongst the Cœlenterata.

Both at its first origin, then, and generally at the present day, this is the function of peristalsis. If now we say, with LANG, that its original function in the Annelida (the statement is not, in LANG's Thesis 21, restricted to Polychæta) was ("perhaps") circulatory, we assume a different origin for the contractions; we renounce the possibility of deriving them from the peristaltic contractions of the alimentary tube of lower forms, which are concerned with ingestion, and must suppose them to have arisen *de novo* for the purpose of circulating the fluid contained in the substance of the gut-wall.

It seems to me preferable to connect the peristaltic action of the intestine in Annelida with similar phenomena in lower forms; to suppose that it existed before the circulatory system was evolved; and to hold, therefore, that its primary object was the movement of matters within the lumen, and that its circulatory function is secondary.

VEJDOVSKY (55, 56), basing his conclusions on refined histological researches, has recently put forward views on the origin of the vascular system in the Annelida which conflict in certain points with the theory of LANG.

Choosing the Enchytreidæ as a starting-point, VEJDOVSKY shows that the perienteric sinus is crossed by thin protoplasmic strands passing between certain basal replacing cells of the intestinal epithelium, which bounds the sinus on its inner side, and a connective-tissue-like membrane which limits it externally; intimately associated with this membrane are a number of flattened, hemispherical, or sometimes stalked cells, which project into the sinus. External to the membrane are the muscular coats of the intestine and the chloragogen layer. The membrane (vasothel) is interpreted as having been separated from the intestinal epithelium, the cells in connection with the vasothel as having migrated outwards from the layer of replacing cells, and the strands which cross the cavity of the sinus as constituting evidence of the original unity of the outer with the inner wall of the sinus. The sinus is therefore contained within the entoderm.

The dorsal vessel possesses two muscular layers, a circular and a longitudinal, continuous with the muscular coats of the intestine. Within these there exists the same vasothel, with the same hemispherical or stalked cells, as was found in the wall of the intestinal sinus; the cells possess processes in which fine fibrils, staining black with iron-hæmatoxylin, are demonstrable; they have, therefore, the character of muscle-cells. The other vessels have a fundamentally similar constitution; the cells of the vasothel, however, may assume different forms, such as, for example, an elongated pear-shape in those cases where they are aggregated to form valves, a cubical shape where they form the rod-like cardiac body.

In the higher families (Tubificidæ, Megascolecidæ, Lumbricidæ, as represented by *Rhyuchelmis*, *Pheretima*, and *Dendrobaena*) the constitution of the vascular system is essentially the same as in the Enchytreidæ.

VEJDOVSKY sums up the theoretical conclusions to be drawn from his observations as follows:—"Sie zeigen vor allem, dass der sog. Darmblutsinus die ursprünglichste Komponente des Gefässsystems vorstellt und dass dieser Sinus ein integrierender

Bestandteil des Entoderms ist. . . . Das Darmepithel nach aussen eine cuticulaartige Basalmembran absondert, zwischen welcher und dem Darmepithel sich die Blutflüssigkeit ansammelt. Doch bleiben einzelne Zellen des Epithels durch lange Fortsätze mit der Basalmembran in Verbindung, namentlich auch die amöboiden Ersatzzellen des Entoderms. In dem Masse nun, wie durch die Assimilationstätigkeit der Darmzellen sich die Blutflüssigkeit vermehrt, erweitert sich der Blutsinus an der Basis des Darmepithels und es lösen sich einzelne amöboide Ersatzzellen aus dem Verbande derselben los und erscheinen dann als selbständige Komponenten der äusseren bindgewebigen Umhüllung (der ursprünglichen Basalmembran). . . . Auf diese Weise liegt der Darmblutsinus im Entoderm selbst und seine äussere bindegewebige, dicht unter der Muskulatur des Darmes sich erstreckende Umhüllung wird als Vasotheil bezeichnet, dessen Zellen mit Kernen höckerartig in das Lumen des Sinus vorspringen und auf diese Weise auf ihren entodermalen Ursprung hinweisen. Das durch eine Delamination des Entoderms entstandene Vasotheil ist daher die ursprünglichste Umhüllung der Blutbahnen.

“Aus dem Bisherigen geht soviel hervor, das der sog. Blutsinus aus dem Entoderm hervorgegangen ist, indem sowohl sein Inhalt, nämlich die hämoglobinhaltige Blutflüssigkeit, wie die äussere Umhüllung, das Vasotheil, vom Darmepithel abzuleiten ist. Da ferner die Hauptblutbahnen, wie das Herz und das Bauchgefäss einfache Differenzierungen des Blutsinus vorstellen, muss sich in erster Reihe auch das Vasotheil an deren Bildung beteiligen. . . . Diese innere Ausstattung verbreitet sich aber auch in die später sich bildende Seitengefässe, ja sie tritt auch in die Capillaren hinein.” And finally, “Das Gefässsystem stellt einen Hohlraum *sui generis* vor, welcher weder vom Blastocöl, noch Schizocöl abgeleitet werden kann und füglich als Hämocöl bezeichnet wird. Trotzdem kann man hier keine Neubildung erblicken, indem die ursprünglichen Bestandteile des Hämocöls, die Blutflüssigkeit und deren äussere Umhüllung, das Vasotheil, vom Entoderm herkommen.”

VEJDovsky's first contribution (55), from which the above is taken, was called forth by LANG's "Trophocöltheorie," to which it is opposed on the majority of essential points. The two authors agree that the origin of the vascular system is to be sought in the accumulation of fluid at the base of the layer of intestinal epithelium, but thereafter they part company. LANG holds that the original position of the fluid is between epithelium and surrounding muscular layer; VEJDovsky that it is within the epithelial layer itself, since it is limited externally by the basement membrane of the epithelial cells and by certain, originally amöboid, replacing entodermal cells which associate themselves closely with the membrane. LANG holds that when definite blood-vessels are differentiated and separated from the sinus, they, so to speak, leave behind them the entodermal epithelial layer; their walls are now constituted solely by muscular or at least mesoblastic cells, and there is therefore no epithelial layer bounding their lumen, within the muscular layer of the vascular wall; VEJDovsky constantly finds a thin membrane, with associated cells, lining the lumen of the blood-vessels within the

muscular layer, which membrane and cells he derives from the entoderm, within which the original development of the vascular system took place. And while LANG considers the cardiac body of certain Enchytræidæ, the valves and the blood-corpuscles—*i.e.* cells or cell-aggregates which occur within the lumen of the vessels,—as ingrowths from outside the blood-vessel, VEJDovsky holds that these are special developments of the cells of the entodermal lining membrane.*

VEJDovsky's work, being entirely histological, has not so many points of contact with mine as has LANG's; nevertheless, a reference to it was unavoidable, and will be equally incumbent in the future on any writer who considers the origin of the vascular system. It will suffice here to draw attention to a few points of fundamental importance with regard to which the views set forth in the present paper are in harmony with those expressed or implied by VEJDovsky. These are—(1) the origin of the vascular system as a space or system of spaces at the base of the layer of intestinal epithelium (not necessarily within that layer); (2) the consequent importance of the recognition of the perienteric plexus as the primitive constituent of the vascular system; (3) the derivation of the musculature of at least the chief vessels from the muscular coats of the alimentary canal.

A paper by FREUDWEILER (18), who had not then seen VEJDovsky's first contribution, immediately succeeded the appearance of the latter; the histological results of the authoress are opposed to those of VEJDovsky. VEJDovsky upholds his former conclusions in a second contribution (56); still more recently STERLING (52) also disagrees with VEJDovsky's results. But since my work is purely from the side of physiology and comparative anatomy, it does not fall within my province to discuss this aspect of the matter further.

II. INTESTINAL RESPIRATION IN POLYCHÆTA.

1. HISTORICAL.

In dealing with intestinal respiration in the Oligochaeta, it was possible to compress into a very small space all previous references to the subject. In the Polychæta, on the other hand, intestinal respiration, or, to speak more broadly, respiration through the alimentary wall, is a well-recognised phenomenon; and it may therefore serve a useful purpose if, before detailing my own observations, I devote a separate section to a summary account of previous contributions.

Three modes are known in which respiration may take place through the lining of the alimentary canal—(1) by the introduction of water or air through the mouth; (2) by the introduction of water through the anus into and along a ventral groove in

* VEJDovsky's view with regard to the blood-corpuscles would be more exactly expressed by saying that he considers them to be descended from isolated entodermal mesenchyme cells, while other similar mesenchyme cells gave rise to the cells of the lining membrane. The blood-corpuscles would thus be descended from the same source as the lining cells, but not from those cells themselves (*loc. cit.*, p. 162).

the intestine; (3) respiration through the general intestinal epithelium, in the way described for the aquatic Oligochaeta.

(1) *Respiration by means of the anterior part of the alimentary tract (especially by œsophageal diverticula).*

QUATREFAGES (37) stated so long ago as 1850 that in certain species of Polychæta the digestive tube appears to aid the skin in carrying out the function of respiration. A small Syllid was seen frequently to swallow large gulps of water, which it subsequently returned by the mouth a little at a time; and the same, but in a less pronounced degree, was seen to happen in *Dujardinia*. On one occasion the intestine of a living specimen of *Hesione pantherina* was observed to be partly distended with gas, which was from time to time expelled either by the mouth or by the anus. The same author subsequently (38, p. 70, vol. i.; p. 92, vol. ii.) refers again to his previous observations, and adds that the quantity of air in the intestine of the *Hesione* was such as to cause the animal to float; he considers it probable that the introduction of air into the alimentary canal was an act voluntarily performed for the purpose of respiration.

EISIG (16) refers to this observation of QUATREFAGES on *H. pantherina*, and to the fact that CLAPARÈDE had found bubbles of gas in the alimentary canal of *H. sicula*. Specimens of this latter on being killed often expel bubbles of gas from mouth or anus; the species is, moreover, often found floating at the surface, the body swollen owing to the distension of two air-containing diverticula of the alimentary canal. These gas-bladders open into the stomach (the region of the alimentary canal between pharynx and intestine), and extend forwards along the sides of the pharynx; they are very extensible, and are contractile both spontaneously and in response to stimuli. The intestine of this species is also capable of energetic contractions; the application of any stimulus is followed by a more or less extensive peristalsis, which, if the intestine is filled with gas, may force this gas with great force into the bladders or into the œsophagus. The bladders are not vascular in *H. sicula*, but in *Tyrrhena claparedii*, a related form, they are vascularised in a manner similar to the intestine.

Similar vesicles, the T-shaped glands of other authors, are found in the Syllids. In *Syllis aurantiaca* they are hammer- or T-shaped, and distensible; whether they are vascular or not is not stated. The greater number of Syllids have only slightly developed or no air-bladders.

Discussing the physiological value of these structures, EISIG states that neither food nor secreted matters are ever found in them, but only a varying amount of clear fluid, or gas, both of which can be pressed out of the stomach into the bladders, or *vice versâ*. The fluid is sea-water, and its purpose is respiratory. Though long and carefully watched, the animals were never seen to take in air; hence the gas must be secreted by the animal, probably in the intestine; and it is probably oxygen, which becomes mixed with carbon dioxide and nitrogen through the respiratory processes. A parallel is drawn with the swim-bladders of fishes.

The swim-bladders of Annelids are therefore to be considered as appendages of the

alimentary canal, whose chief function is to store up the oxygen secreted by the intestine, in order that it may be used at need, alone or mixed with sea-water, for vicarious respiration. They are, however, of necessity also hydrostatic.

In the Syllids, the bladders are best developed in what are apparently the more primitive forms; in the more modern genera they seem to be disappearing, perhaps because their respiratory function is being replaced by that of the general surface of the body. The peculiar appendages of the alimentary canal in *Nereis* are probably homologous. Finally *Phyllodoce*, though possessing no bladders, may be observed at times to have a large quantity of gas in its intestine. It is to be noted that Hesionids, Syllids, Phyllodocids, and Nereids have no gills.

In conclusion, "alimentary respiration constitutes a function which belongs in greater or less degree to the whole group of Annelids, and indeed represents, along with cutaneous respiration, the most primitive form of respiratory activity. We may accordingly suppose that, as a preponderating cutaneous respiration has led to the development of external appendages in the form of gills, so a preponderating alimentary respiration has led to the development of bladders."

Observations on the respiratory vesicles of Syllids were subsequently published by DE ST JOSEPH (14), who controverts some of EISIG's conclusions. This investigator also often saw Syllids swallow both air and water (this is definitely stated for *Syllis alternosetosa* and *S. prolifera*); other specimens were seen whose intestine contained both air and water at the time of examination; and in others again air was seen to be expelled by mouth or anus. These observations were made in many cases on forms which have no "air-bladders"; hence the ingestion of air and water does not depend on the presence of these organs.

The bladders are not "swim-bladders" (*i.e.* are not hydrostatic in function), since when expanded they are filled with water, never with air. The hydrostatic function is performed by the intestine; thus the Syllids which were oftenest observed floating (species of *Trypanosyllis* and *Eurysyllis*) have no bladders, but show constrictions of the intestine, with intervening pockets in which the air is contained. The author considers the true seat of production and reservoir of the gas to be the intestine, which extracts the air from the sea-water as EISIG thinks (EISIG's idea is, however, rather that of a definite secretion of the gas by the intestinal epithelium), or into which the air penetrates directly, by the mouth.

In a subsequent instalment of the paper (15) similar observations on other families are described. *Leptonereis vaillanti* (Lycoriidæ) sometimes puts forth its proboscis in order to take in air and water, which are received into two extensible respiratory appendages of the stomach. The Phyllodocids also aspirate air and water through their extended proboscis. In *Magalia perarmata* (Hesionidæ) there are no swim-bladders; the distensible ventriculus and the intestine, however, may contain air and water introduced through the proboscis. *Oxydromus propinquus* often projects its proboscis, swallowing air, water, and small particles within its range; these are then

forced into the ventricle, and this contracting in its turn passes the air and water into the intestine, whence they are expelled either through the proboscis or anus. The same was observed in *Kefersteinia cirrata*.

MALAQUIN (30), like DE ST JOSEPH, never saw the ventricular caeca of Syllids distended with air, not even when the animals were taken floating; accordingly he too denies EISIG's conclusion that they can function as hydrostatic organs. He describes the sucking action of the proventriculus (the cylindrical portion of the alimentary canal in front of the ventricular caeca); this is peristaltic in nature, a progressive diastole from front to back being followed by a progressive systole. The animal frequently rejects the water which it has taken in in too large quantity by similar series of contractions executed in the reverse direction.

The caeca cannot be considered as special glands, since the epithelium, though secretory, has the same structure as that of the anterior intestine; their secretory function is thus identical with that of this portion of the alimentary tube, and in no way peculiar. As has been seen, they are not swim-bladders; they must therefore be considered as reservoirs to contain the surplus water taken in by the mouth; when they are absent, the anterior portion of the intestine serves this purpose.

Respiration is thus not solely cutaneous; the swallowed water is an indication of the respiratory importance of the intestinal epithelium. This, however, must not be exaggerated; the ventricular caeca, when they exist, being reservoirs of water, may play a more important part than the intestine in the discharge of the respiratory function.

SCHAEPPi (41), after noting that *Ophelia radiata* has no gills in the anterior part of its body, describes the whole anterior portion of the gut—the œsophagus and especially the stomach—as being characterised by an extremely rich folding; the gut sinus extends into these folds. “Now it is known that especially in mud-dwelling worms alimentary respiration is an essential complement to cutaneous and branchial (or specialised cutaneous) respiration; and I am convinced that this factor is not to be neglected in *Ophelia*, where over a large region the lumen of the gut is reduced by this folding to a labyrinth of narrow clefts.” He concludes that the blood is oxidised in these folds; the oxidation process, which is carried out in the hinder region of the body by gills, is thus effected in the anterior by the gut. Since nothing is said about the mode of introduction of respiratory water into the œsophagus and stomach, it would seem that SCHAEPPi conceives it as entering at the mouth.

SALENSKY (40) describes the pharyngeal sacs of *Polydora* (Spionid) as five symmetrical evaginations of the wall of the alimentary canal, resembling in their manner of formation the gill-pouches of Enteropneusta and Chordata, with which they are probably homologous. These pouches are found also in *Saccocirrus* and *Polygordius*. It is not stated that they are homologous with the T-shaped glands of Syllids; and nothing is said regarding their physiological value.

BOUNHOL (5, 6, 7) is acquainted with the respiratory function of the anterior part of the alimentary canal in Syllids; his papers are mainly concerned with quantitative

determinations of oxygen and carbon dioxide, and so do not directly touch the present subject.

(2) *Respiration by the introduction of water at the anus into a ventral groove of the intestine, or into a ventral groove and accessory intestine.*

The chief source of our knowledge of this phenomenon is EISEN's work on the Capitellids (17).

In *Notomastus*, a worm about four or five inches long, a ventral ciliated groove begins at the anus, and extends forwards for a distance of two centimeters; here an accessory intestine (Nebendarm), which may be regarded as the forward continuation of the groove, separates from the gut, which it accompanies on its ventral side as far as the posterior end of the œsophagus, where it again joins the alimentary tube. This accessory channel lies close to, or at some distance from, the intestine; in the latter case it is connected with the intestine by a sheet of peritoneum. It has the same structure as the intestine; it contains no food, but may be filled with structureless matter cast off by the lining cells; its epithelium is furnished with minute cilia, which are recognisable only with difficulty. The groove in the posterior part of the intestine is provided with long cilia, which work in an ascending direction—an arrangement probably serving to introduce into the accessory gut water which enters the intestine at the anus. The animal possesses gills; intestinal respiration is therefore not of such importance here as in *Capitella*, which has none.

Dasybranchus is similar; so also is *Mastobranchus*, in which the accessory gut keeps close to the intestine. In *Heteromastus* the connection is still closer; here the cavity of the accessory gut often bursts through into the intestine, and sections may thus show the "Nebendarm" merely as a groove of the intestinal wall.

In *Capitella* the intestinal groove is well marked, and extends through one-third of the body length; its epithelium is high and markedly ciliated. The accessory gut lies close to the intestine, and here also often appears, through the solution of the separating layer, as a ventral groove of the intestine. It is continued forwards by an œsophageal groove, lined by a low epithelium, which is ciliated either only very faintly or not at all. In this animal the hinder portion of the intestine frequently contracts rhythmically, or in a "pumping" fashion. The ciliary current can often, especially in young animals, be followed upwards as far as the region of the "Nebendarm." *Capitella* may sometimes be seen to wave the hinder end of its body about in the water, like certain aquatic Oligochæta; it has no gills, and so depends entirely on cutaneous and intestinal respiration.

Generally in this family the accessory gut has a diameter about one-fifth that of the intestine, with which it corresponds in structure. It never contains food; but it may, like the intestine, be filled with a spongy mass which has been cast off by the epithelial cells.

The question of the comparative anatomy and homologies of the accessory gut, discussed at some length by EISEN, lies rather apart from our present subject. We may briefly

note his reference to the fact that SPENGEL found in *Oligognathus* and other Eunicidæ a tube which apparently ends blindly behind, and anteriorly opens further forwards than the "Nebendarm" of Capitellids, at the anterior end of the jaw-sac; it differs also in having no muscularis. In larval Eunicidæ KLEINENBERG found both anterior and posterior openings into the gut. In general, the accessory gut appears to be a separated neural intestinal groove; the separation may be more or less complete, various stages being exemplified in the various genera of the Capitellidæ. Its occurrence in two families so widely separated as the Eunicidæ and Capitellidæ shows that it is an essential feature of Annelid organisation (dass in ihm ein dem Annelidentypus inhärentes Organ vorliegt), a view to which we are forced also by the recognition of homologues of the "Nebendarm" in other groups; as such may be mentioned the notochord (EHLERS), the accessory intestine of Gephyrea, and the similar structure in Echinoderms (EISIG).

On the subject of intestinal respiration in general, EISIG repeats his former views (*vide supra*). In a large number of Annelids the chief part of the respiratory function is performed by the intestinal wall, and this is especially the case in those forms which are without specific respiratory organs. In such there may actually be a collection of gas (oxygen) in the intestine; and in some, even special reservoirs (so-called swim-bladder-like organs) may be formed to contain it. In many Annelids, again, the separation of the nutritive and respiratory activities of the gut has been secured by the provision of a deep groove, with an ascending ciliary current, in the posterior portion of the intestine; this groove may extend along the whole of the intestine, or may be separated from the main channel as a "Nebendarm." Hence the latter arrangement is to be considered as a means of bringing water destined for respiratory use to the œsophagus without interfering with digestion and absorption; and this is especially to be seen in the gill-less *Capitella*, where there is also an œsophageal groove. No other function has been assigned to the accessory gut of Annelids and Gephyrea; AGASSIZ, however (without adducing any evidence), supposed that of Echinoderms to be excretory, though PERRIER, probably rightly, considers it to be respiratory.

Lastly, EISIG, rejecting the division of the Chaetopoda into Polychæta and Oligochæta, considers the Capitellids as closely related to Oligochæte forms, and endeavours to explain the absence of the accessory gut in Oligochæta. In the terrestrial Oligochæta its absence is of course comprehensible. As to aquatic forms;—if it were to be shown that these represented the more primitive Oligochæta, it would be difficult to understand why they, so closely related to the Capitellidæ, have dispensed with a "Nebendarm"; especially as they have to rely (except *Alma nilotica*) entirely on cutaneous and intestinal respiration. But marine Oligochæta are descended from terrestrial forms; and it is possible that the same applies to the freshwater Oligochæta too.

In EISIG's account of the physiology of the accessory gut, and in his theoretical conclusions presented, though in a much compressed form, above, there are many points

on which it would be interesting to dwell. Since, however, the purpose of this section is historical, I must content myself with the following remarks.

In viewing the accessory gut as a means of bringing respiratory water to the œsophagus, EISIG, influenced probably by his previous work on the T-shaped glands of Syllids, apparently considers the anterior part of the alimentary tract of Polychæta as that in which the respiratory function, when it exists, is specially and necessarily localised. But there is no necessity for respiratory water to reach the œsophagus in order to be of use; the posterior portion of the gut is throughout the Chaetopoda far more generally respiratory than the anterior. The fact is, that one or two cases where the function of respiration is discharged by the anterior part of the alimentary tube have attracted special attention, while the much more widely distributed respiratory activity of the hinder intestine has received comparatively little notice.

One might, I think, ask for more evidence that this respiratory water reaches the œsophagus; the current in the intestine was followed, under favourable circumstances, as far as the posterior end of the accessory gut, but I have not found any mention of a current within the "Nebendarm," the cilia of which are minute and with difficulty recognisable, and which, moreover, may be blocked by a structureless mass. Indeed, the respiratory value of the "Nebendarm" at the present day, whatever may have been its original use, would almost seem to be doubtful.

EISIG's last point is that the "Nebendarm" has disappeared in the Oligochæta because this group was originally terrestrial; the present aquatic Oligochæta, that is, are aquatic secondarily, and have no accessory gut because their terrestrial ancestors lost it. That marine Oligochæta are always descended from terrestrial forms, as EISIG states, is certainly not in all cases true; *Clitellio arenarius*, one of the best examples of a marine Oligochæte, can hardly be anything else than an originally freshwater Tubificid which has become habituated to a new environment. Moreover, alimentary respiration, by the introduction of water at the anus (though without an accessory gut), is in fact present in most aquatic Oligochæta; if the aquatic Oligochæta were in general descended from terrestrial forms, this respiratory activity of the intestine would have been lost, in the same way as EISIG supposes the accessory intestine to have been lost.

The absence of the accessory intestine in the majority of Chaetopoda needs no special explanation. The only thing that need be said is that it has never been present. We may agree that the possession of intestinal respiration is a primitive feature; we must, however, recognise that an accessory intestine is not a primitive character at all, but one of high specialisation. The aquatic Oligochæta, and a large number of Polychæta, show the less specialised condition, diffuse respiration by means of the whole circuit of the intestinal wall; some forms show a degree of specialisation, in possessing a more markedly ciliated ventral intestinal groove, along which the introduced water passes upwards; and further progress may result in the separation of an accessory gut.

The foregoing account of EISIG's work almost exhausts the literature which falls to be referred to under this head. GAMBLE and ASHWORTH (20, 20A) find that there is in

Arenicola a ventral groove running the whole length of the intestine: this is probably, according to the authors, the morphological equivalent of the siphon of Capitellids, but they see no reason to regard it or any other part of the alimentary canal as respiratory in function; the cilia work towards the anus. CERRUTI (12) has found in *Microspio mecznikowianus* a ventral groove in the intestine, which he regards as the equivalent of the accessory gut of other Annelids; the ciliary current in the posterior portion of the intestine is directed forwards, and the water thus introduced appears to serve a respiratory purpose.

(3) *Respiration through the general internal surface of the intestine, by means of the introduction of water at the anus, but without specially differentiated mechanism.*

Detailed observations on this mode of respiration in Polychæta, as in Oligochæta, are almost wanting. I have, however, met with a number of isolated statements, couched usually in general terms, which show that the phenomenon is generally recognised, even though the extent of its occurrence has not yet been investigated.

Thus QUATREFAGES (38), referring to his observations on the swallowing of air and water by Syllids and Hesionids (*cf. ante*), introduces the subject by saying: "The digestive tube either in its entirety or in some portion of its extent also appears to me to be able to take an active part in respiration." It is possible that he may have had in mind a general activity of the intestinal wall in the manner above specified, though he makes no further mention of it.

EISIG (17, *cf. supra*) speaks of diffuse alimentary and cutaneous respiration as being the primitive form. I have not, however, found any recognition of the fact that this diffuse alimentary respiration is still widely existent in present-day forms; and in his earlier paper (16), speaking of "an animal which normally respire by means of a stream of water driven through its alimentary canal," the stream is evidently conceived as entering at the mouth.

MALQUIN (30), though furnishing a detailed account of the intestine of Syllids, makes no mention of its respiratory function. He notes that the posterior part of the intestine is more transparent than the anterior portion, and is ordinarily yellow; the epithelium here is not secretory, and is always strongly ciliated (in his fig. 35, Pl. viii., the cilia are shown directed posteriorly, and are presumably meant to be working towards the anus). He mentions that CLAPARÈDE had previously observed refractile concretions in this part of the intestinal wall, and had hence, supposing it to be excretory, called it the "urinary portion" of the tract. The results of keeping the animals in water containing carmine and fuchsin are given: "The only part of the digestive tube to be distinctly coloured is the posterior intestine; here are situated the youngest cells, *i.e.* those most favourably constituted for the manifestation of osmotic phenomena. The posterior intestine seems thus to be the principal seat of absorption of matters elaborated by the anterior and middle portions of the tube. It also seems to be an organ for the arrest of non-assimilable products; which explains the presence of the numerous urinary concretions found in the two lateral grooves of its wall." It

is strange that MALAQUIN does not mention the ascending ciliary current in the posterior part of the intestine of many of these forms; and that he does not consider the possibility that the colouring matter of his experiments, which was deposited in the wall of the posterior intestine, might have been directly introduced at the anus.

LANG (29) mentions that STEEN observed antiperistaltic contractions of the intestine in *Terebellides stroemii*, and WIRÉN similarly in a number of families of Polychæta. GOODRICH (22) is acquainted with the postero-anterior action of the intestinal cilia in Syllids.

I may add two references to general zoological treatises. GEGENBAUR (21) says: "The hindgut of many Annelids may be seen to take in water, and this may be connected with a respiratory function of this division of the intestine." Similarly, BENHAM (4): "Many Chaetopods take in water by the anus—no doubt for respiratory purposes—and pass it forwards along the intestine."

2. OBSERVATIONS ON POLYCHÆTA.

Though the third of the modes of respiration specified in the foregoing section is much the commonest and most widely distributed in the Polychæta, it is the one which has hitherto, as may be seen from the historical account, received the smallest amount of attention, at least in print. Students of the group are probably, indeed are almost necessarily, familiar with it; but the details of the process, and its actual distribution, have received no extended treatment.

The following observations deal for the most part with this mode of respiration,—with respiration through the general internal surface of the intestine, by means of the introduction of water at the anus, but without specially differentiated mechanism. It may, however, be noted here that the mode of alimentary respiration which occurs in *Aphrodite aculeata* is not strictly to be included under any of the three headings previously enumerated; in this animal the respiratory water, though expelled from the anus, is not taken in there, but at the mouth, and passes as a regular and voluminous current through the whole of the alimentary tract. I have also included some observations on the phenomena to be seen in the posterior portion of the intestine of *Capitella capitata*, though I have nothing to add concerning the "Nebendarm."

The observations here recorded are distributed over the majority of the families of Polychæta. They could, of course, be extended, and it was my object so to extend them as to include representatives of at least all the more accessible British families; but an unfortunate attack of illness cut short my time at Plymouth, and so prevented me from carrying out my plan in full.

SYLLIDÆ.

Trypanosyllis zebra.

In a specimen which was undergoing asexual division, ciliary action in an ascending direction, so violent as to be seen with a small dissecting microscope, was observed in

the last ten segments; it very possibly existed higher up in the alimentary canal also, but this could not be definitely ascertained, owing to the presence of opaque genital products in this region; it was, however, present, and very violent, in the hinder part of the anterior of the two animals in course of separation.

An experiment with carmine particles was not successful; the animals seemed to try to get away from the carmine, as if the particles irritated them.

No antiperistaltic contractions of the intestine were observed.

Odontosyllis ctenostoma.

When the anus was open, the ascending ciliary motion was actively present at the anus, feebler a few segments higher up the intestine; it died away in one specimen at the tenth segment above the anus; in another it was visible for eleven segments, and was then obscured by masses of faecal matter in the intestine.

When the anus was closed, the ciliary action ceased near the anus, but was still faintly visible higher up.

Antiperistaltic contractions of the gut were not observed.

Eusyllis tubifex.

Reversed ciliary action was proceeding actively and could be observed with ease in the last nine segments; above this level the intestine was too opaque to allow of its being observed, but from the fact that the action was still proceeding strongly at the point where it ceased to be visible, it may be concluded that it extended some distance further up.

The intestine was seen to contract from time to time, though infrequently and irregularly; and whenever the intestine contracted, the dorsal vessel was also seen to contract. The impression given was that both structures possessed independent contractility, though, as said, the contractions of both were always simultaneous.

Genus *Autolytus*.

In a specimen of *Autolytus pictus*, in which the anus was almost closed and the lumen of the hinder part of the intestine considerably contracted, ascending ciliary action was observed in the last few segments; but this was only momentary, since the anus was quickly closed and the lumen of the hinder part of the gut occluded. In another specimen the phenomenon was not observed at all.

In a species of this genus which was perhaps *A. prolifer*, the anus was closed during the time the animal was under observation; ascending ciliary action was seen in the eighth, ninth, tenth, and eleventh segments in front of the anus, perhaps most markedly in the ninth and tenth, though it could not be called obvious anywhere.

No antiperistalsis was observed. The dorsal vessel was, however, contracting; its contractions are thus quite independent of those of the gut (if these latter ever occur).

In another species of the genus, of which several specimens were examined, the conditions varied. In two specimens ascending ciliary action was absent; in a third there was no ciliary movement near the anus, which was closed, but some distance up the alimentary canal an obscure ascending ciliary action was visible. There was no antiperistalsis in any of the specimens; in one the dorsal vessel was seen to be contracting regularly; so that here also the vascular contractions are quite independent of any contractions of the intestine.

In another species, probably belonging to this genus, the ascending ciliary movement was observed at the hinder end of the last animal of a chain. No antiperistaltic waves were seen; contractions of the dorsal vessel were however going on rapidly and at regular short intervals (once every four seconds). Another specimen of the same species showed neither ciliary movement nor antiperistalsis; it is therefore not to be concluded that reversed ciliary action does not occur in a species because it does not happen to be observed in a particular specimen.

Other Syllids.

A number of other Syllids were examined, but not specifically identified. As representative of these observations the following may be recorded.

In a Syllid with well-developed ventricular cæca and well-marked sucking action of the pharynx, ascending ciliary action in the intestine was not visible at first, but could be distinguished later; it could be made out in nearly all the hinder transparent segments of the intestine, though the anus was kept closed during the whole observation. Antiperistaltic contractions of the gut were also taking place,—at first in the hindmost fourteen segments, but later much further forwards also; these contractions were quite irregular in rhythm; each wave extended usually over only a few segments, though sometimes over a larger number,—as many as eight; sometimes a contractile wave would begin at the posterior end of the animal, sometimes a few segments in front of this, sometimes further forwards. These contractions of the gut were sufficient to constrict the lumen very considerably; and they and the contractions of the dorsal vessel were quite independent.

In other species also some degree of ascending ciliary motion was observed in the last segment, or last two segments, of the intestine.

The above are all cases in which ascending ciliary motion, with or without ascending peristaltic contractions, was observed in the intestine. In many Syllids, however, these phenomena do not occur, or at least did not occur during the time the specimens were under examination. This was the case in *Syllis gracilis*, as well as in a number of animals which were not specifically identified.

HESIONIDÆ.

Castalia punctata.

A considerable number of specimens were examined. It may be noted that the intestine is, considering the small size of these animals, remarkably opaque; and in most specimens it is only in a few segments at the posterior end that the intestinal canal is sufficiently transparent to allow ciliary motion, if present within it, to be distinguished. Nevertheless the appearances are often striking.

In specimens examined under a coverslip, the anus is often seen to be closed; the posterior part of the intestine may also be contracted, and its lumen obliterated; and in such cases ciliary action is of course absent. During the examination, however, the anus may be seen suddenly to open, and the intestine to dilate; a violent ascending ciliary action then becomes visible in the hinder intestine, beginning at the anus and extending upwards till obscured by the opacity of the intestinal wall.

In some cases the anus may be open, and the ascending ciliary action may be observed, throughout the examination; while in others the anus may be closed and ciliary action absent. Sometimes even with the anus closed, ascending ciliary action may be seen within the intestine in one or two segments at its hinder end. In one case the ciliary action was downwards, towards the anus, in the last four segments, while above this it was in the reverse direction for the small distance—about two segments—which intervened before the intestine became too opaque to allow of observation.

The above paragraphs recapitulate observations made at Plymouth. In a number of Hesionids examined at Millport, which were probably also specimens of *Castalia punctata*, exactly similar phenomena were observed;—violent reversed ciliary action with open anus, visible as far as the intestinal wall was transparent; a fainter ciliary motion, near the anus only, when the anus was closed. Small particles were seen to be drawn to the anus and taken into the intestine. In each of two specimens examined, a string of yellowish mucus was seen to be passed out without interruption of the ciliary action; in one case part of this string was drawn in again, apparently through its getting towards the side of the anal aperture and so coming within the action of the ciliary current (*cf. ante*, p. 744).

Antiperistaltic contractions of the intestine are also to be observed, but are very variable. They may be absent altogether; or a few irregular antiperistaltic waves, of moderate amplitude, may be seen beginning at the anus or sometimes further forwards; these pass over a few segments and then cease. In one specimen antiperistalsis was observed to occur throughout the greater part of the length of the body; the contractions were, however, irregular and intermittent, and afterwards subsided altogether.

In no case was any connection observed between the antiperistaltic waves of the intestine and the contractions of the dorsal vessel.

APHRODITIDÆ.

Aphrodite aculeata.

Three specimens, which had been in captivity for a week, were used for the following series of observations and experiments. They were examined in an oblong glass dish containing a quantity of sand, in which they half buried themselves.

The hinder end of the animals is, when they are quiescent, turned up, or even somewhat recurved over the body; the margins of the flat and sole-like ventral surface are approximated to each other some little distance from the (morphological) posterior end of the animal, so that the appearance of a spindle-shaped aperture is produced, whose sides are formed by the hindmost portions of the margins of the ventral surface with the neighbouring setæ. Owing to the hinder end of the animal being bent upwards as above described, this apparent aperture faces upwards and backwards, and its actual upper or anterior end is the morphological posterior end of the body. The appearance is characteristic, but I cannot find that it has any functional importance, and I have described it only because the spindle-shaped gap might, on a cursory examination, be mistaken for the anus. The anus is, when closed, an inconspicuous crescentic slit, concave backwards, on the dorsal surface just in front of the posterior end of the animal.

If, now, one of these animals be closely watched, the following succession of events will probably be found to occur. From time to time the approximated margins of the posterior portion of the ventral surface, which together have the spindle-shaped outline described above, diverge; the hinder end of the animal is in some degree depressed, as when a dog with an erect tail puts it down; the anus opens, and appears for about the length of two seconds as a conspicuous circular aperture, now looking upwards; the anus then closes again, the tail is erected, and the posterior end of the ventral surface resumes the appearance of a spindle-shaped slit.

During the time when the anus is open, a jet of water is being expelled. This may be shown in several ways. Thus if the surface of the water in the dish be carefully watched, it will show a fountain- or jet-like elevation immediately above the anus at the moment when the anus is open. Behind one of the specimens, in which the posterior end was quite flat and not erected, and in which therefore the anus when open faced backwards, a little heap of sand was placed during the interval between two expulsions; this heap was blown away by the next jet expelled from the anus. Or carmine particles suspended in the water may be used to demonstrate the current. Both the quantity of water expelled and the force with which it escapes are obviously considerable: even when the animal is in water of some depth, a jet is raised on the surface at the moment of expulsion.

The hinder end of the animal is not always erected; when the animal is crawling about it may be quite flat. The object of erection is probably to keep the anus above

the level of the sand, in which the specimens partially embed themselves when they are free to do so.

The appearances above described may be seen to occur both when the animals are at rest and when they are moving. They may be absent after a long period of quiescence,—for example, in the morning, when the specimens have probably been motionless for some time; in this case the animals seem to need wakening up before the phenomena can be manifested; after the animals have been handled and made to crawl about, the expulsion of water begins in the way described.

The interval between successive jets of a series is very fairly regular in the same animal, but it varies in different animals, or at different times in the same animal; in four observations it was 22, 13, 13, and 18 seconds.

The question remains to be answered, Where is this water taken in? It seems most natural, having in view the phenomena of intestinal respiration in other Annelids, to suppose that it enters at the anus in the intervals between the jets. This however is not the case. During the intervals the anus is closed; and even granting that a minute quantity of water might possibly be introduced between the lips of the anus by means of ciliary action, this would be very far from furnishing, in the few seconds available, the considerable amount ejected.

The next possibility is that the water is both sucked in and ejected during the time the anus is open,—first rapidly sucked in, then immediately expelled. The jet on the surface, however, makes its appearance directly the anus opens; in the experiment where a wall of sand was built up behind the animal, the sand was blown away quite at the beginning of the open period; and observation, even under a lens, with carmine particles in the water, fails to detect any inhalant currents at the anus at any period of the cycle.

It would seem, therefore, that since the water is not introduced at the anus, it must enter by the mouth. The following experiment was next performed:—A specimen was left for half an hour in water containing carmine in suspension; it was then taken out and washed, and put into a white dish with clean water; it was now observed that the water ejected from the anus was carmine-tinted. After about six jets, when things began to be a little obscured, the contents of the dish were replaced by clean water; it was then easy to see that the fluid expelled from the anus was still coloured. The water in the dish was again renewed after another five jets, again after five more, and again after about six more jets, the ejected water being tinted throughout. Finally, after about six further jets had been expelled, the animal was once more placed in clean water, and observation against the white background showed that the ejected fluid was still slightly coloured. A considerable amount of water containing carmine must therefore have been present in the alimentary canal when the specimen was first placed in the clean water; and the double series of intestinal cæca in this species at once suggest themselves as its probable receptacle.

If, now, an animal, while regularly expelling water from its anus, be placed in a

shallow dish and only partly covered with water, so that, while the anus is immersed, the back projects above the surface, it can be seen, by carefully inspecting the dorsal surface, that each expulsion of water is accompanied by a depression of the middle of the animal's back, in the middle third or in the third quarter of the body, reckoning from the front. In the intervals this region slowly arches itself and becomes slightly convex, to become flat or slightly concave again at the expulsion of the next jet. The mechanism of expulsion would seem to be the contraction of the muscles of the body-wall, especially those of the dorsum.

Direct proof that the water is taken in at the mouth is furnished by the following experiment:—The anterior part only of an animal, which previously was ejecting quite colourless water from its anus, was immersed in carmine water for fifteen minutes. It was then washed and put in clean water; ten jets of carmine-tinted water were then expelled from the anus. The water in the dish was then changed; similarly after four more jets, and again after four more. The tint of the expelled water was now growing fainter, and after the water had been again replaced, and three more jets had occurred, no colour was perceptible. Another similar experiment gave similar results.

DARBOUX (13), investigating the alimentary canal of *Aphrodite*, found no solid food in the intestinal diverticula; SETTI (44), however, found traces of solid matter. Later, JORDAN (26) agrees with DARBOUX that no solid food enters the diverticula. We may therefore conclude, from these observations and those recorded above, that respiration by means of the alimentary tract is a prominent feature in *Aphrodite aculeata*; it takes place in a peculiar manner, by the introduction of water in considerable quantity at the mouth, and its passage through the alimentary canal, from which it is ejected in jets by the anus. The intestinal cæca probably act as reservoirs of the ingested water; and its expulsion is effected principally by the muscles of the dorsal body-wall.

Other Aphroditidae.

A number of small Polynoids were examined microscopically, and experiments with carmine in suspension were carried out on *Halosydna gelatinosa*, a larger species, but the results were in all cases negative.

Phyllodocidae.

I have observed a large number of Phyllodocids, mostly small specimens suitable for microscopic examination. In none, however, was any sign of ascending ciliary action to be seen; carmine experiments also gave negative results.

Antiperistalsis was observed on one occasion only, and then only slightly; a few feeble antiperistaltic contractions extended over two or three segments in the posterior part of the body; they were irregular in rhythm, and soon ceased.

NEREIDÆ.

Nereis pelagica.

I examined at Millport a number of small specimens of *Nereis*, which belonged to the common species of the place, and which appeared to correspond most closely to *N. pelagica*.

Except in one instance, no reversed ciliary motion in the intestine was observed, though the anus might be open. The exception was a headless specimen, possibly though not certainly of the same species, in which a faint ascending ciliary action was observed in the posterior part of the intestine, the anus being open.

On the other hand, antiperistalsis, though in a few it might for a time be in abeyance, was noted in every specimen examined. The contractions may be regular and strong: in one case, with a rhythm of six per minute, the waves progressed slowly forwards, taking about four seconds to traverse one segment: during the first part of this observation the contractions started not at the anus but at the seventh segment from the posterior end; later, however, a series of extremely active contractions began quite at the hinder end of the animal. In the headless specimen mentioned above, antiperistalsis was regular, strong, and very evident: the waves proceeded at the rate of eleven per minute, and could be followed for thirty-two or more segments from the posterior end. In other cases the contractions, beginning at the anus, may be well marked and regular, but may be limited to a few segments only.

In some specimens antiperistalsis is less well marked. Though easily visible, it may be gentle and discontinuous. In other cases the contractions may be slight or hardly noticeable, irregular in rhythm and limited in extent, and may occur some distance in front of the anus. In two specimens the movements were seen to cease altogether for a time.

The relation of the contractions of the dorsal vessel to the antiperistaltic waves is variable. As a rule none exists. The antiperistalsis may be feeble, or irregular, while the dorsal vessel is beating strongly and regularly. The contractions of the dorsal vessel persist when antiperistalsis is temporarily in abeyance. Or though both series of contractions may be proceeding regularly and strongly, they may be quite independent of each other; those of the dorsal vessel may be three times as frequent, and much more rapid in their passage.

In one case, however, where the antiperistalsis began at the anus, and ceased as such a few segments in front of this, it appeared to be continued forwards as a contraction of the dorsal vessel: the wave propagated itself forwards not along the intestinal walls, but along those of the dorsal vessel, as happens regularly in *Eolosoma* and the *Enchytræidæ* (cf. Part I.). The connection between the two series of contractions, intestinal and vascular, was maintained for periods of perhaps half a minute, and then would be broken, to be resumed again shortly afterwards; and so on. The rhythm of the contractions was fairly rapid—about once in four seconds.

Leptonereis vaillanti.

So far as I have observed, ascending ciliary movement does not occur in this species.

In one specimen the anus was seen to open rhythmically at short intervals. Following on each closure of the anus, after a very slight pause, an antiperistaltic wave began at the anus and progressed up the intestine. The series ceased after a short time; the animal was under compression during the examination, in a small quantity of water.

In another specimen, only irregular contractions of the posterior part of the intestine were observed. In a third, nothing was seen.

EUNICIDÆ.

Ophryotrocha puerilis.

No ascending ciliary current was visible in the intestine. In one specimen very large cilia were seen to be in violent motion around the anus, towards which their action was directed.

Antiperistaltic contractions were seen to take place regularly in about the posterior third of the body; starting at the anus, they occurred every few seconds, passing slowly forwards through eight or nine segments. The waves were of considerable amplitude, the lumen of the canal being narrowed by the contraction to about one-third its usual width. The contractions did not seem to occur when the animal was completely quiescent, but appeared to be started by any slight movements.

No connection was noted between intestinal and vascular contractions; indeed, contractions of the dorsal vessel were not observed.

Hyalinocia tubicola.

Neither phenomenon was observed; this, however, is not conclusive, since the specimens had to be chloretoned into quiescence before an examination could be undertaken. Still the animals did not give one the idea that anything of the kind was to be expected.

ARICIIDÆ.

Examples of this family, probably belonging to the genus *Scoloplos*, were examined at Millport. Reversed ciliary action was not observed.

Antiperistalsis was present in all the specimens examined. In the three specimens observed it was most marked in, or even confined to, the middle segments of the body.

The vascular contractions, in each of the two cases where they were observed, were independent of the antiperistalsis. Thus in the first specimen, where both series of contractions were very well marked, the vascular series was about twice as frequent as the intestinal, and the passage of the wave along the dorsal vessel was more rapid than that of the antiperistaltic contraction along the gut.

SPIONIDÆ.

The only observation that I have to record for this family refers to *Nerine vulgaris*. Antiperistalsis was present; but there was no relation between the contractions of the dorsal vessel and those of the intestine.

CHÆTOPTERIDÆ.

Chætopterus variopedatus.

This animal is of some size, and the interior of the alimentary canal cannot be observed with either a dissecting or an ordinary microscope; hence the examination presents a certain amount of difficulty. The following methods were adopted:—

A specimen was placed on a glass plate and the posterior end covered with an ordinary glass slide. The compression was sufficient to flatten the hinder part of the animal fairly well; and the very end of the alimentary canal was then transparent enough to allow a violent ascending ciliary motion to be seen with the dissecting microscope. Around and outside the anus, ciliary motion is obvious and violent, at times apparently not acting in any definite direction, at others working towards the alimentary canal.

Carmines in suspension was now run under the covering slide. This, or the prolonged experimentation, occasioned a considerable discharge of mucus, which caused the carmine to aggregate into small flocculi. A slow current towards the end of the intestine, beginning some little distance away, and gradually increasing in swiftness as it approached the anus, was thus made visible. Some of the carmine accumulated in small masses round the anus; but the large majority of smaller particles were carried with some violence into the intestine, while a few were possibly deflected and helped to swell the flocculi near the margins of the orifice.

The specimen was now placed for 25 minutes in a dish containing water with carmine in suspension, and afterwards again examined. A fair-sized flocculus of carmine particles was now seen to be hanging out of the anus; this had probably been forced out of the intestine by the manipulations necessary in moving the animal. This flocculus was slowly drawn into the intestine while the animal remained under observation. Fresh carmine added formed flocculi with the mucus excreted from the surface of the body, and those flocculi which came in contact with the lobes round the anus were slowly drawn over them and through the margins of the anus into the intestine. Smaller particles were also drawn in, but notably the larger ones, and small flocculi, as described.

The question suggested itself whether the mucus might not normally have the function of entangling particles to be subsequently ingested by the anus. But it is hardly likely that this is a principal object of its secretion, since it is formed over the whole surface of the body.

No antiperistaltic contractions were observed.

OPHELIDÆ.

Ammotrypane aulogaster.

In this species it is improbable that any considerable amount of respiratory exchange can take place through the integument; the form is cylindrical, the body is not segmented externally, the parapodia are obscure, and the surface is smooth and shiny and resembles that of a Nematode with its thick cuticular investment. The dorsal cirri function as gills; but they are simple small finger-like inconspicuous processes.

The posterior end is peculiarly constituted. It is funnel-shaped, a deep conical depression leading down to the anus; the mouth of the funnel opens ventralwards. RATHKE (39) describes it as follows:—"Der After stellt eine nach unten offene Schaufel dar, deren Rand mit kurzen Cirri besetzt ist; eine ähnliche Bildung kenne ich nur bei *Nais digitata*, wo sich jedoch die Schaufel nach oben öffnet." I may add that the posterior margin of the funnel is more vascular than the rest, as evidenced by a red blush which marks this region; the hinder part of the intestine also, in contrast to the rest of the canal, is distinguished by a deep-red blush.

The carmine experiment gave an interesting result. The funnel was facing upwards during the observation; into it the carmine particles were gently and equably drawn, and then travelled forwards towards or into the intestine. Some particles travelled in a posterior direction along the upper (in this position) surface of the animal's body for a very considerable distance before doubling over the margin and entering the funnel. The entering current was regular and definite, and some of the particles introduced were of fair size.

The observation was conducted under the dissecting microscope, and the above appearances were seen on focussing the upper strata of the anal region. On focussing for a lower level, approximately the middle of the funnel, an equally definite and regular return current was observed. At a deeper level again, particles of carmine came into view which had sunk to rest on the lower wall of the funnel; these were agitated by ciliary action, but I did not note a regular entering current along the lower inner surface of the funnel corresponding to that along the upper.

There can be no doubt that the entering current is caused by ciliary action; but the worms are of some size (two inches long), and opaque; and higher powers than those afforded by a dissecting microscope could not be used. Hence the only direct observation of the existence of cilia was that of the agitation of the carmine particles which had sunk on to the lower part of the inner surface of the funnel.

ARENICOLIDÆ.

Arenicola ecaudata.

This species is too large and opaque for ordinary microscopical examination; though the observation of small specimens, and even of larger ones by compression between glass plates, will reveal a certain amount of the organisation of the living animal.

Ciliary motion in the intestine of course could not be made out.

The anus may be seen, in specimens under observation in a dish, to be periodically held open, sometimes widely, then closed, opened again for a time, closed, and so on. The animal may at the same time continue pushing its hinder end about, as if it were using it to explore with.

In the middle part of the body, which is fairly transparent under pressure, a well-marked antiperistalsis of the intestine was noted; in a second specimen this manifested itself as a continuous antiperistaltic ripple, which began gently about segment xviii. and ended at about segment vi., behind the pharynx. Antiperistaltic contractions were never observed in the hinder part of the intestine; possibly because most of the specimens were quite opaque here, and so could not have manifested it in any case. Hence, though the observer receives the impression that "mouthfuls" of water are being taken in at the anus, the proof that any water is passed up the intestine by antiperistalsis is wanting. The description may, however, be compared with what happens in *Leptonereis* and *Capitella* (pp. 799 and 803).

The antiperistalsis is unconnected with the vascular contractions; these are more frequent, and pass along much more rapidly.

FLABELLIGERIDÆ.

Siphonostoma diplochaitos.

In the single specimen of this worm which I have had the opportunity of observing, the anus was held open, but the lumen of the gut was contracted—it might be said to be absent. It was therefore impossible to say whether an ascending ciliary action ever occurred or not. There was no evidence of any ciliary movement outside the anus.

A perienteric sinus surrounds the intestine, and this, in the compressed animal, was much wider than the proper alimentary tube within it.*

A well-marked antiperistalsis, regular, rapid, and frequent, began at the anus. The lumen of the intestine being already constricted to the point of disappearance, this could obviously not affect the diameter of the canal, and could subserve only the propulsion of the fluid in the sinus; but presumably at other times the condition would be that of the Enchytræidæ or of *Æolosoma* (cf. pp. 749, 751, 752), where alimentary antiperistalsis and vascular contractions are one and the same thing. The anatomical relations also correspond to those of the Enchytræidæ: there is no dorsal vessel in the intestinal region, but the ventral vessel extends to the hinder end of the body.

CAPITELLIDÆ.

Capitella capitata.

The anatomy and physiology of the accessory intestine have been described, in accordance with EISEN's account, in the historical section. My observations do not

* FUCHS (19), describing the vascular system of this worm from a paper by JAQUET, speaks of lacunæ in the intestinal wall, but says that he is unable to make out from that author whether there is a perienteric sinus or not.

touch on these points, but are concerned with the phenomena which lead one to infer a general respiratory activity of the whole wall of the posterior portion of the intestine. Specimens were found in large numbers at Millport, and a considerable number were examined. It may be mentioned that the animals frequently progress with the posterior end of the body first.

The existence of a ventral ciliated groove in the hinder part of the intestine, posterior to the accessory gut, has been mentioned previously. Ascending ciliary action is, however, by no means confined to this groove; the whole circumference of the intestine in its posterior part shows the same ciliary action. The anus is often opened widely for a moment, and then closed; or it may be held widely open for some time—perhaps 20 to 30 seconds,—and it is at such times that the ciliary action is specially obvious. Whether it occurs in the middle region of the body or not cannot be seen, owing to the opacity of the intestine under the microscope in this portion of its extent; at the point where it ceases to be visible it may be indefinite in direction. In the œsophageal groove also (*vide ante*), ciliary action is well marked, but does not work in any definite direction.

Antiperistaltic contractions of the intestine are almost always visible. The waves may be seen to extend, in a quiescent animal, from the anus to the anterior end of the hinder section of the intestine, or some distance in front of this. In other cases they are more restricted in extent. They may begin at the anus and extend forwards for only a few segments, and their rhythm may be irregular. Or they may occur only in the anterior segments of the intestine, just behind the thorax. Or they may occur in the same animal, at various portions of the intestine; or lastly, the contractions sometimes manifest themselves as merely ring-like constrictions of a segment of the gut, which do not progress, but, remaining stationary, after a time relax again.

CIRRATULIDÆ.

Cirratulus sp.

In specimens belonging to the genus *Cirratulus* observed at Millport, ciliary action was seen around the anus, and particles of carmine in the neighbourhood were agitated and apparently attracted; some of the particles seemed to be taken into the gut. The animals are however too opaque to allow the presence or absence of ciliary action in the intestine to be determined.

An antiperistalsis of the same character as in *Arenicola ecaudata* was observed; and the anus was opened and closed in the same manner as has been described for that species.

TEREBELLIDÆ.

Polycirrus (? *caliendrum*).

Ascending ciliary action was seen in this species just within the anus.

A more interesting phenomenon, however, and it would seem a more effective means

of propelling water along the intestine, is the antiperistaltic action of the intestinal walls. The contractile waves begin at the anus, and proceed upwards for a considerable distance—about one-third of the length of the body. They are regular and strong; their amplitude may be illustrated by saying that in diastole the intestine almost fills the body-cavity, while in the contracted condition it is reduced to a mere cord, the lumen being occluded. In the middle third of the body also there are to be seen frequent antiperistaltic waves which occlude the lumen of the canal; they are not however continuations of the posterior series, which do not get as far forwards as this.

The anus is opened fairly widely at intervals corresponding to those of the intestinal contractions, and is regularly closed at the beginning of each antiperistaltic wave. Thus there is a sort of gulping action; the antiperistaltic contractions appear to pass forwards the water which has been taken in at the open anus.

This action was illustrated by the behaviour of a mass of faecal matter, which while being expelled was partly drawn in again. Carmine particles introduced near the anus are rapidly aggregated into flocculi by mucus; these flocculi were also sucked in at the anus; some were actively expelled shortly afterwards. A large mass of carmine was also drawn in, and after ascending the intestine for a few segments was rapidly shot out again. Another mass sailed in and immediately ascended about six segments up the intestine. Minute particles were wafted in in numbers.

The carmine experiments do not prove that the matter—the solid matter, at any rate,—which is taken in at the anus ascends the intestine for any great distance; the particles did not by any means reach the anterior limit of the antiperistaltic waves. From the forcible way in which the larger particles were expelled, it seemed as if there was an active rejection of such masses; and it is possible that water containing only substances in solution, or, at most, minute particles of solid matter, is propelled upwards to a considerable distance. Such at least is the impression given by the gulping action of the anus and the very strong and regular antiperistalsis of the intestine.

Genus *Amphitrite*.

In a species belonging to this genus examined at Millport there was no evidence of reversed ciliary action in the intestine; antiperistaltic contractions occur, similar to those described above in *Polycirrus*.

In a young semi-transparent specimen, performing slow writhing movements in a dish, the anus was seen to be periodically opened and somewhat everted, appearing almost trumpet-shaped; after a short time it was retracted and closed, and at the same instant an antiperistaltic wave started from the anus and passed forwards for some distance. The sequence of events gave the impression that a gulp of water had been taken and was being passed along the intestine.

Carmine particles in suspension also enter the intestine, and may reach a distance equal to a quarter of the length of the body from the anus.

Genus *Terebella*.

A number of young specimens of *T. nebulosa*, found at Millport, were small enough to be examined microscopically.

In the specimen in which the appearances were best marked, ciliary motion was not seen within the intestine; round the anus, however, it was obvious, and though it did not seem to give rise to a current in any definite direction, some small particles appeared to enter the anus, which was held open.

Antiperistaltic contractions began at the anus and extended the whole length of the intestine; they were slow and fairly ample. A perienteric sinus is present in the walls of the gut, very narrow posteriorly, but wider in the anterior part of the intestine; in this latter region the lumen of the gut is not affected by the contractions of the muscular coat, which thus act only on the fluid contained in the sinus; in the posterior region the contractions are not merely circulatory in their effect, since here they also cause a narrowing of the lumen of the intestine.

T. lapidaria, examined at Plymouth, shows no definite evidence of any intake of fluid; a few carmine particles entered the anus, but their entry seemed to be a matter of chance.

AMPHARETIDÆ.

Melinna sp.

A number of examples of a species of *Melinna* were observed at Plymouth.

Ascending ciliary action may be seen just within the anus; the animals are too opaque to allow of its being followed far, but it can be successfully demonstrated by the carmine experiment. The anus is frequently held open; and at such times carmine particles may be seen slowly to approach the anus, and then rapidly to enter; particles resting on the surface of the body near the posterior end may be seen to move backwards in a line, as if connected together by an invisible thread, and then to round the hinder end of the animal and enter the anus, travelling along and clinging to the surface all the way.

Antiperistaltic contractions of the intestine may also be observed in the posterior and middle regions of the body. They may begin at the anus, or at a more anterior point. In the specimens observed, which had been in the laboratory for over a week, they were irregular in rhythm.

SABELLIDÆ.

Genus *Potamilla*.

Examples of two small species of *Potamilla* were examined at Plymouth: the larger of the two was perhaps *P. reniformis*, the smaller probably *P. torelli*.

In the smaller of the two species ascending ciliary action was observed in the majority of specimens. In one case it was well marked, indeed violent, in the last three

and a half segments; the anus was open, and the lumen of the gut widely patent. Small particles were carried into and rapidly up the intestine, then were forced downwards for some distance, again carried up, and so on; the downward recoil of the particles was apparently due to a series of spasmodic contractions of the intestinal wall in the fourth segment from the end; the whole of the rest of the canal in this specimen was altogether quiescent. In other cases, for example those in which the anus was kept closed during the examination, ciliary motion was feeble or absent.

Antiperistaltic contractions of the intestine are almost always to be observed; they are usually only circulatory in their effect, *i.e.* they affect only the contents of the perienteric sinus, and are not violent enough to cause any narrowing of the lumen of the alimentary canal. The contractions may extend in regular series over the whole intestine to within a short distance of the head; or they may be irregular and discontinuous.

In the larger of the two species the anus was, in the specimens examined, kept closed and the lumen of the posterior part of the gut almost occluded. Reversed ciliary action was not observed. The antiperistaltic contractions of the intestine were circulatory only in their effect, and had no influence on the already contracted lumen of the gut. Two striking peculiarities of this animal, which must impress every observer, are its mode of locomotion, and the use it makes of its posterior end in exploration. There are two clusters of small eye-spots, one on each side of the anus; this end of the body is continually active, exploring in all directions, and it is always this end which it protrudes, when possible, from under the edge of the cover-slip. This, and the continual slow-crawling locomotion, always with the anal end first, unite in making it appear as if this were the anterior end of the worm; while the gills—dragged behind, folded like a closed umbrella—seem like projections from its hinder end.

Dasychone bombyx.

The phenomena are similar to those in *Potamilla*. A reversed ciliary movement could be followed from the anus upwards for about six segments, though the posterior part of the intestine was considerably contracted; small particles were seen to be taken in at the anus. The antiperistaltic contractions (in this condition of the intestine at least) are entirely circulatory in their effect.

In some Sabellids examined at Millport, but not identified, similar phenomena were observed. Ascending ciliary movement was present, either restricted to the most posterior section of the intestine, or extending upwards through its hinder and middle thirds,—in the latter case, violent at its hinder end, and visible even when the worm was viewed as an opaque object under the low power of the binocular. Antiperistalsis was present over the whole intestine, or was absent in its middle third; in any case, its effect was mainly circulatory.

ERIOGRAPHIDÆ.

Myricola dinardensis.

Ciliary motion was observed in this species throughout the greater part of the intestine, from the anus to the beginning of the stomachal dilatation; in places it was indefinite in direction, but on the whole it was, as usual, ascending. The anus was closed during the time of examination; it is perhaps a fair assumption that if it had been open the ciliary action would have been much more obvious and definite.

Antiperistalsis was observed to extend throughout the intestine, as far forwards as the second setigerous segment. Its character varied at different times and in different regions; at times a regular and fairly strong series of contractions in the middle region of the body markedly constricted the lumen of the intestinal canal; at other times their effect was confined to the perienteric sinus, the lumen of the gut being scarcely narrowed at all.

The physiological importance of the posterior end of the body is as marked as in *Potamilla*. In addition to the lateral rows of eye-spots, the animal possesses a pair of clusters of such spots at its anal end. This end, too, resembles a worm's head in shape; the animal continually uses it for exploration, turning it from side to side, retracting it, trying another direction, exactly as a worm does with its head. The animal always crawls with this end in advance; indeed, the posterior end obviously is, in a physiological sense, the animal's head; the other end, the morphological head, is merely dragged behind, and is quite passive. It may be added that BENHAM (4) states that *M. infundibulum* also moves tail first.

SERPULIDÆ.

Spirorbis borealis.

Ascending ciliary action was seen in all the specimens examined. As an example, the appearances may be described in an animal in which the alimentary canal was at first in a contracted condition in the whole of its posterior portion. Though violent ciliary action was observed outside the anus, none could be seen inside the intestine, and, the anus being closed, no carmine particles were taken in. After some time the anus opened, and a violent ascending ciliary action was then visible in the intestine. By varying the focus of the microscope, currents to and from the anus could be seen; at one level, all the carmine particles were being swept towards the anus; at another, the motion of the particles was for the most part directed away from the anus. A few carmine particles were seen to enter the intestine, but they never seemed to ascend very far, and were usually soon rejected; the animals often give the observer the impression that they shrink from the touch of solid particles. It may perhaps be inferred that the anus is normally used for the ingestion of fluid only (cf. *Polycirrus*).

Similar phenomena were noted in other specimens. In one, a mass of faeces in the

posterior part of the intestine was seen to be continually rotating round the longitudinal axis of the canal (cf. *Eolosoma viride*, p. 744 *ante*).

No antiperistalsis was observed in any of the specimens. It must however occur, at least in the form of contractions of the gut-wall which effect the circulation in the perienteric sinus; FUCHS (19) speaks of a contractile intestinal sinus in this family.

Pomatoceros triqueter.

This species is too opaque to be easily examined. Ascending ciliary action may however be seen at and for a short distance above the anus, even though the anus and lumen of the intestine are much contracted. In one specimen the anus was seen to open and close from time to time—about eight times per minute, but irregularly—and the ascending ciliary action was more easily to be observed while the anus was open.

Intestinal antiperistalsis occurs, but in different degrees at different times and places; in the posterior part of the body it was, in one specimen, circulatory only in its effect, *i.e.*, while causing constriction or obliteration of the perienteric sinus, it did not influence the calibre of the intestinal lumen; in the middle region of the body of another specimen, however, it caused a marked narrowing of the lumen of the canal.

ADDENDUM ON SIMILAR PHENOMENA IN CERTAIN OTHER GROUPS.

I subjoin a few observations on related groups, made in the course of my work as opportunity offered.

Archiannelida.

During my stay at Plymouth I was kindly supplied with specimens of *Dinophilus taniatus* and *Histriobdella homari*.

Dinophilus taniatus, though a small animal, is very opaque, and the observation of the interior of the alimentary tract is not easy. Ascending ciliary motion was observed in a number of specimens, but it was never as obvious or as violent as in certain of the Polychæta or Oligochaeta.

As an example, a specimen may be cited which showed this phenomenon for a considerable distance up the alimentary canal from the anus; for a short space above this, ciliary motion was present in an ascending direction on the left side of the intestine, in a descending direction on the right; and just behind the stomach it was entirely descending. Later, this ciliary action was ascending in direction in the anterior part of the intestine, especially at the junction of intestine and stomach, but near the anus its direction was indefinite.

Many variations were met with, especially with regard to the extent and direction of the ciliary currents in the stomach and anterior portion of the intestine. In some cases no ciliary motion could be detected, but this was, in all but one specimen, because the intestine was full of solid matter.

Antiperistaltic contractions of the intestine seem to be absent. In one case they were observed in the posterior portion of the stomach.

Specimens of *Histiobdella homari* yielded negative results. Slight ciliary movement was observed in the last part of the intestine, but it was directed towards the anus, which was kept closed. Irregular contractions of the intestine occurred, but not definitely in either direction.

It may be added that the intake of water by the anus is a recognised occurrence in *Polygordius*; and that GOODRICH has observed ascending ciliary action in *Nerilla* (22).

Nemertinea.

While engaged at Millport in working at the Nemertines of the Clyde, I took the opportunity of examining all the species I came across (in most cases numerous examples), in order to determine whether or not similar phenomena occurred in that group. The results were mostly negative; the anus is a very small orifice, and is usually invisible even by the microscope; it is never held open, and consequently there is no possibility of the entrance of water for respiratory purposes. Ciliary movement was never visible within the alimentary canal. A few infrequent antiperistaltic waves were seen to pass along the posterior part of the intestine in *Lineus gessnerensis*; and this phenomenon was present, and better marked, in *Cephalothrix linearis*. In this species the waves are sometimes sudden and sharp, at other times slow; they are capable of forcing solid masses up the gut for some distance; they are not, however, continuous over long distances, but are rather fragmentary, each one being confined to a limited portion of the tract. Direct peristalsis occasionally occurs, but is much less frequent.

These observations are of interest, because *Cephalothrix* is perhaps one of the most primitive genera of Nemertines, and because it is the one in which the blood-vessels also are most obviously contractile.

SUMMARY.

One or more species belonging to each of nineteen families of Polychæta were submitted to examination. The main results of the observations may be outlined in the table which follows (p. 810).

This table may be compared with that constructed for the aquatic Oligochaeta (p. 744). A few remarks on certain points may be added.

(1) In considering the frequency of ascending ciliary action in the intestine, it is necessary to exclude from the enumeration several of the above families. In the Arenicolidae, Flabelligeridae, and Cirratulidae, the conditions (size, opacity, contraction of intestinal canal) did not allow of observation of the interior of the intestine; all that can be said is that there is a slight probability in favour of its occurring in the Cirratulidae, and no reason either for or against in the other two families. In the

Family.	Ascending Ciliary Action.	Antiperistalsis.	Relation between Antiperistaltic and Vascular Contractions.
Syllidæ	Yes	Yes (not very common)	Simultaneous (<i>Eusyllis tubifex</i>).
Nesionidæ	Yes	Yes	Independent.
Aphroditidæ	Special arrangements for intestinal respiration (in <i>Aphrodite</i>); circulatory system much reduced.		
Phyllodocidæ	No	Practically absent	
Nereidæ	Yes (slight)	Yes	Variable; mostly absent.
Eunicidæ	No	Yes	No relation observed.
Aricidæ	No	Yes	" "
Spionidæ	?(No note)	Yes	" "
Chaetopteridæ	Yes	No	
Opheliidæ	Yes	?(No note)	
Arenicolidæ	?(No observation possible)	Yes	No relation observed.
Flabelligeridæ	?(" ")	Yes	Antiperistalsis is mainly circulatory.
Capitellidæ	Yes	Yes	(Circulatory system much reduced.)
Cirratulidæ	?(No observation possible)	Yes	?(No note).
Terebellidæ	Yes (slight)	Yes	Antiperistalsis is mainly circulatory (in <i>Terebella</i>).
Ampharetidæ	Yes	Yes	(Probably as in <i>Terebellidæ</i>).
Sabellidæ	Yes	Yes	As in <i>Terebellidæ</i> .
Eriographidæ	Yes	Yes	" "
Serpulidæ	Yes	Yes	" "

Spionidæ I have unfortunately no note as to whether it occurs or not. Excluding these four families, the phenomenon occurs, not in all, but in some, members of eleven families out of fifteen.

This, however, very possibly understates the case. The phenomenon is variable—sometimes absent or ill marked, and sometimes well marked, in the same species, or even in the same specimen; and it may occur in one species, and not (so far as observed) in a related species (*e.g.* among the Syllidæ). It is possible, therefore, that it might have been observed in families in which it is recorded as absent, if other species or even other specimens of the same species had been examined.

The ascending ciliary action is often visible when the anus is closed, and may even be distinguishable when, in addition, the intestine is itself so much contracted as almost to occlude the lumen. It is, however, usually much more marked when the anus is open (*e.g.* *Odontosyllis*, *Castalia*, *Capitella*, *Potamilla*, *Spirorbis*, *Pomatoceros*); and sometimes, as for example in *Castalia punctata*, the relaxation of the anus, in a specimen in which it has been closed for some time, resembles nothing so much as the opening of sluice-gates in a watercourse.

That the effect of the ciliary action is to produce an upward current in the fluid contents of the alimentary canal, and to cause the entry of water at the anus, if the anus is open, will be at once admitted. The appearances are conclusive to anyone who examines such forms as *Castalia*, *Capitella*, *Chaetopterus*, and certain Syllids, Sabellids, and Serpulids, or who has tried the carmine experiment with *Ammotrypane*, *Melinna*,

or *Chaetopterus*. A peculiarity about these carmine experiments, however, deserves notice. The experiment may fail altogether to demonstrate an entering current at the anus, and this although a violent ascending ciliary action is going on all the time;—compare the account of *Trypanosyllis zebra*; the animal seems to try to get away from the carmine. In other cases, though the carmine enters, it seems never to ascend very far, and soon to be rejected (compare the accounts of *Polycirrus* and *Spirorbis*). It would appear that the posterior end of the intestine is not fitted to deal with solid particles, and that if possible it avoids receiving them.

(2) Antiperistaltic contractions of the intestine are even commoner than ascending ciliary action. Of the nineteen families before enumerated, the Opheliidæ, concerning which I have no note, are to be excluded; of the rest, it appears to be absent only in the Chaetopteridæ, of which, however, very few specimens were examined, and probably in the Aphroditidæ, which have (at least *Aphrodite aculeata* has) special arrangements for intestinal respiration; for practical purposes it may also be reckoned as absent in the Phyllodoceidæ. It occurs therefore in fifteen families out of eighteen.

That a phenomenon which occurs so widely and constantly, in so large a group as the Polychæta, has some essential significance, will be immediately admitted. That in a number of forms, both of Oligochaeta and Polychæta, the contractions are partly circulatory in their effect, driving forward the fluid in the perienteric plexus or sinus, is obvious; that they are even mainly circulatory in some (Enchytraeidæ, Sabellidæ, Serpulidæ, etc.), is no less true. These facts have already been insisted on, and have an essential place in the speculations on the manner of evolution of the vascular system which have been already put forth.

But that this is the fundamental meaning of antiperistalsis appears to me to be an error. The question is discussed at length on pp. 779–781 *ante*. The association of antiperistalsis with ascending ciliary action; the fact that the waves obviously cause (in most cases) a considerable constriction of the alimentary tube, and are hence much more violent than is necessary merely to propel the fluid in the intestinal vascular network; and that the function of peristalsis generally in the animal kingdom, including the groups from which the Annelida may be supposed, directly or remotely, to be derived, is to propel the contents of a tube along its lumen; are among the arguments there adduced in support of the view that the reversed peristalsis of the intestine had originally, and in many cases has still, a respiratory or at least ingestive significance, and that this is the essential meaning which underlies the phenomenon. I may here, in addition, recall the periodical opening and closing of the anus (gulping action), and especially the direct association of this with the starting of an antiperistaltic wave from the anus (*Leptoneris raillanti*), which in *Polycirrus* and *Amphitrite* may be fairly described as a regular gulping and swallowing of “mouthfuls” of water.

(3) Associated with this use of the anal end of the body are several other phenomena which, like that, induce us to believe that this extremity has in many cases a greater physiological importance than would naturally be attributed to it. Eye-spots occur by

the side of the anus in *Potamilla*. *Capitella* frequently, the Eriographidæ (*Myxicola dinardensis*, *M. infundibulum*), and Sabellidæ (*Potamilla*) regularly, move with the posterior end foremost; and this manner of locomotion, along with the evidently highly developed sensibility and the continual exploring movements of the anal extremity, indeed the whole behaviour of these worms (*Myxicola* and *Potamilla*), makes it impossible to resist the belief that the physiological head of the animal is the morphological posterior end of the body.

(4) I have already mentioned that my object in studying the Polychæta was to extend the observational basis on which the views, previously put forward, on the origin and mode of evolution of the vascular system in the Annelida were founded. The results of my investigations are evidently in harmony with those views, and in a general way confirmatory. Since, however, they add nothing of importance to the argument, it seemed better to develop the discussion on the basis of the Oligochæta, and to give the results of the Polychæte investigation separately, as has been done in the present Part.

The reasons why the material gathered from the lower families of the Oligochæta is better adapted to serve the purpose of a discussion on the evolution of the vascular system seem to be the following:—In the first place, the Oligochæta are distributed into far fewer families than the Polychæta; the anatomical material which falls to be considered is therefore more easily mastered, and, when mastered, is more easily arranged. Secondly, the Microdrili are for the most part small transparent worms which can be observed microscopically without difficulty; while the Polychæta are often large and opaque, and hence the points in question—ascending ciliary action, antiperistalsis, the relation of intestinal to vascular contractions—are often impossible of discovery by ordinary means. Thirdly, the aquatic Oligochæta appear to contain a larger number of the lower stages of the evolutionary series; indeed, it may be said that they represent a generally more primitive level than any of the Polychæta.

Since, therefore, it appears that the observations on the Polychæta fit into the scheme of evolution of the vascular system as already outlined, and that thus there is nothing that contradicts, and much that agrees with, the results arrived at from a study of the Oligochæta, it does not seem too much to say that the views previously put forward receive a useful confirmation from this series of observations.

A few parallels with the Oligochæta may be noticed.

(a) In the Serpulimorpha (Sabellidæ, Eriographidæ, Serpulidæ) there is a perienteric sinus within the muscular coat of the intestine, but no differentiated dorsal vessel behind the œsophagus; the ventral vessel, however, exists throughout the length of the body (I take these anatomical data from FUCHS). Here the antiperistaltic contractions of the muscular coat drive forwards the blood in the sinus; they have usually, however, comparatively little effect in narrowing the lumen of the gut. The anatomical and physiological conditions are comparable to what is found in the Enchytræidæ, and represent one of the lower stages in the evolution of the vascular system, one in which the vascular is, in great part of its extent, not emancipated either anatomically or

physiologically from the alimentary system. *Siphonostoma* and *Terebella* may also be compared.

In some ways, however, the course of evolution has led in the Serpulimorpha to a more specialised state of things than that seen in the Enchytræidæ. In the Enchytræidæ the "sinus" is probably a close network (*cf.* note on p. 778); in the Serpulimorpha it appears to be really a continuous sinus; this is, according to the views put forward in the present paper (p. 778), a secondary condition, which has been developed out of that of a network by the fusion of adjacent channels. Secondly, the antiperistalsis is mainly circulatory in its effect; it usually constricts the lumen of the gut but little, and can therefore have only a slight influence in moving the fluid in the interior of the intestinal tube. This is to be both compared and contrasted with the results of evolution in the Naididæ and Tubificidæ; as in these latter the antiperistalsis becomes limited in its effects to the dorsal vessel, the main circulatory channel in the intestinal region, and the cavity of the gut is but little affected, so here also the effects of the antiperistalsis are confined to the sinus, the main component of the circulatory system in this region, and the lumen of the gut is affected only slightly.

(*b*) The phenomena observed (*vide ante*) in one specimen of *Nereis pelagica* are interesting as indicating the occasional persistence of a primitive condition of things in a group where the vasenlar system has progressed to a high evolutionary level. In this specimen antiperistalsis began at the anus, travelled forwards for a few segments, and was then continued on without interruption as a contraction of the dorsal vessel. The same wave was at the hinder end a general antiperistalsis of the intestinal wall, further forwards a contraction of the dorsal vessel,—a temporary relapse to an earlier physiological condition or stage of evolution (*cf.* *Aelosoma* and the Enchytræidæ), and indicative of the original unity of the two phenomena.

(*c*) *Eusyllis tubifex* is also noteworthy. In the Syllidæ, according to FUCHS (19), the dorsal vessel is unconnected with the intestinal canal, although it is sunk within a fold of the gut-wall; though there is thus apparently a close spatial relation, complete anatomical differentiation has taken place, and the dorsal vessel is not merely a special channel in the intestinal plexus. On referring to the foregoing observations, it will be seen that in the Syllidæ no relation was found to exist, as a rule, between antiperistaltic and vasenlar contractions—indeed, antiperistaltic contractions were not often visible; the physiological condition corresponds with the anatomical. In a specimen of *Eusyllis tubifex*, however, the dorsal vessel contracted whenever the intestine contracted; the physiological unity was in some degree preserved—a condition which again points back to a stage where intestinal and vascular contractions were not only coincident in time, but undifferentiated parts of the same phenomenon.

(*d*) Finally, there is a large number of families in which the condition is that of the higher aquatic Oligochaeta. In *Autolytus* (Syllidæ), *Castalia* (Hesionidæ), the Eunicidæ, Ariciidæ, Spionidæ, and Arenicolidæ, both anatomical and physiological differentiation

are complete ; there is a well-developed dorsal vessel separate from the intestine, and the contractions of the two are quite unrelated to each other.

3. THE BEARING OF THE OBSERVATIONS ON PÜTTER'S THEORY.

The introduction of water at the anus, and its propulsion upwards along the intestine, has throughout the present paper been referred to, in accordance with the usual custom, as a respiratory process. The assumption is that the oxygen carried in solution diffuses from the water through the intestinal epithelium into the fluid contained in the intestinal sinus, or network of capillary vessels in the wall of the gut, while carbon dioxide is given off in exchange.

It has, however, been hinted (p. 776) that other dissolved matters may be thus introduced. There is obviously no reason why, if suitable substances in solution gain an entry into a cavity whose walls have in a special degree, as have those of the intestine, the power of absorption, those substances should not be absorbed, just as the nutritive matters which enter by the mouth and are reduced to solution in the anterior part of the tract are absorbed. Though intestinal respiration is a well-established term, it is at least possible that the process may not be exclusively respiratory.

In these circumstances the views of PÜTTER become of interest. PÜTTER holds that in the case of aquatic animals a considerable part—even the greater part—of their food comes, not from solid matters introduced into and reduced to solution in the alimentary tract, but from the dissolved organic matter of the medium in which they live, which is absorbed, it may be through the alimentary walls, or in other cases through some portion of the surface of the body.

The results of PÜTTER's earlier investigations are conveniently presented by JOHNSTONE (25), from whose work I take the substance of the two following paragraphs:—

PÜTTER found, in the case of the sponge *Suberites domuncula*, that an animal of about 60 grammes weight required per hour 0·92 mgm. of carbon. If the sponge is to obtain its food by eating plankton organisms (LOHMANN's estimates of the density of plankton in the open Mediterranean being assumed true for the bay of Naples), it would be necessary that it should capture, per hour, all the plankton contained in 242 litres of sea-water, that is, about 4000 times its own volume. The volume of water passing through the osculum in this time is, however, only about 300 c.c., and this quantity contains only $\frac{1}{810}$ th part of the carbon required by the sponge.

According to PÜTTER's estimate, the carbon requirements of the animal are contained in a dissolved form in so small a quantity of sea-water as 14·2 c.c. Thus, even if we assume that all the carbon compounds contained in sea-water are not capable of being utilised as food, and that the absorption coefficient is not a very high one, it is still the case that the water circulated through the cavities of *Suberites* may contain enough carbon to supply the animal's requirements. PÜTTER also suggests that the respiratory surfaces of, for example, Molluscs and Ascidians are really surfaces for the absorption

of food-matters. "At any rate, the actual evidence that the gills of these creatures are organs which function in the absorption of foodstuff is just as strong (or as weak) as the actual evidence that they take up dissolved oxygen from solution in sea-water.

"What, then (continues JOHNSTONE), is the function of the alimentary canal in such animals as these? PÜTTER suggests that the surface of the latter is one which is instrumental in the absorption of dissolved food-matter from the sea" (*i.e.* it would have the same function as the gills). "That it should also take in and digest solid food particles, such the organisms of the plankton, may be a secondary function acquired after the alimentary canal has been evolved for the absorption of liquid foodstuff. Thus the capture and assimilation of diatoms by a mussel or a holothurian may be compared with the capture and assimilation of insects by an insectivorous plant; which latter process we may regard as being strictly secondary in importance to the process of feeding by means of photosynthesis of starch by the green parts of the plant."

In later publications, PÜTTER recapitulates his investigations and the conclusions to be drawn from them (34), and extends his theory to include even Fishes (35). Having shown the absorption of dissolved matters in the latter class, he infers that this takes place through the gills; the skin is not apt for absorption, and the fish swallows no water; the quantity of water passing over the gills, however, is enormous—even more than is required for the purpose. The soluble matters capable of being used as foods, which occur in the water, are to be considered as the mainstay of the fish's nutrition.

PÜTTER's last communication (36) deals with certain objections to his views. HENZE had shown that PÜTTER's methods of estimating the amount of dissolved organic matters in sea-water were insufficient, and gave much too high values. PÜTTER admits this, but still holds that the quantity of carbon compounds in solution is enormously greater than that of the living organisms. He returns to the subject of Actinians. It is said that the tentacles are "obviously" for the purpose of taking in solid food. As a matter of fact, says PÜTTER, they are not; small animals or particles of flesh which touch their surface are not seized and introduced into the oesophagus; on the contrary, the crown of tentacles closes over the mouth opening and protects this from the entry of the so-called nutritive particles (E. PRATT, KÜKENTHAL). KÜKENTHAL never observed solid nutriment in the interior of the polyps, nor saw solid food ingested; finely pounded fish-flesh added to the water was not taken up, but the particles were surrounded by a slimy secretion which caused them to adhere to the surface of the colony (but *cf.* CARLGREN's observations, referred to on p. 821 *post*). The gastro-vascular system of corals is, at least partially, excretory of the end-products of metabolism.

PÜTTER concludes: "It has been proved (1) that the quantity of organic compounds in solution in the sea exceeds by hundreds of times that of the animal organisms; . . . (3) that animals can take up dissolved organic substances even when these are present in a concentration of 1 : 280,000 to 1 : 2,000,000; (4) that animals can exist,

which supply at most $\frac{1}{1000}$ of their material needs by digestion of solid food (*Suberites*, *Octocoralla*, *Rhizostomata*); (5) that animals can live and produce ova altogether without solid food, that the progeny grow, undergo ecdysis, and develop at the same rate as animals under the usual natural conditions, all without solid food (MAX WOLFF on *Simocephalus*)."

My observations on the Polychæta and aquatic Oligochæta serve to show that the introduction of water into the alimentary canal by the anus is a much commoner phenomenon than has hitherto been recognised, and hence give some support for the application of PÜTTER's views to these groups.

In this connection it is interesting to consider the exceptions to the rule of the prevalence of intestinal respiration, both in the lower Oligochæta and the Polychæta. In the lower Oligochæta (not counting the Enchytraidæ, which are not principally aquatic) the most marked exception is that of the genus *Chaetogaster*. This is, so far as I know, the only carnivorous group of aquatic Oligochætes; specimens will ingest animals or portions of animals of a relatively considerable size: indeed, they will attempt to swallow animals much larger than themselves. Of the Polychæta, excluding doubtful cases and those in which there is no evidence either way, the families in which, so far as my observations go, ascending ciliary action in the intestine does not occur, are the Phyllodocidæ, Eunicidæ, and Ariciidæ (the Aphroditidæ are not reckoned, their intestinal respiration being of another type). These are all placed in the group Nereidiformia (= Rapacia) by BENHAM, a group composed for the most part of active carnivorous forms with armed proboscis (FUCHS places the Ariciidæ with the Spioniformia).

It is precisely these carnivorous forms which, since they ingest comparatively large masses of solid food, approach nearest in their manner of feeding to such higher animals as birds and mammals. It is possible to suppose, therefore, that these forms are capable of supplying themselves in this way, and do supply themselves, with the required amount of nutriment. The absorption of dissolved matters is no longer necessary; a continual circulation of water through the alimentary tract would even be harmful, as diluting to too great a degree the digestive juices poured out for the purpose of acting on the solid masses. It is comprehensible, therefore, that it should be among these forms that the exceptions to the rule of intestinal "respiration" are found to occur.

III. GENERAL CONSIDERATIONS.

The posterior part of the alimentary canal, with the anus, is in most of the higher animals the channel by which the food-remains are got rid of, and in them it subserves the function of expulsion practically exclusively. But widely distributed, as we have seen, among the aquatic Oligochæta and the Polychæta there is an inhalant function as well; and it is perhaps worth while inquiring whether the expulsive or the receptive function is likely to be the more primitive. In other words, is it probable that such a funda-

mental fact of structure as an anus was first developed in phylogeny for the purpose of getting rid of undigested remains of food?

(1) In the first place, when we consider the Coelenterata and Platyhelminia, it appears that there is no necessary inconvenience in returning undigested matters by the mouth, even in the case of animals of some considerable size. The Ophiurids indeed show us that the anus may be so unimportant as to be dispensed with, even by highly organised animals which at an earlier stage in phylogeny possessed this feature. It might perhaps be argued that it is not size, nor even a generally high level of organisation, that necessitates an anus, but length of body relatively to breadth,—that a long and narrow alimentary canal, as for example in a worm-like animal, will require a posterior outlet, while a short and broad nutritive cavity would not do so; to which it may be answered that many of the Turbellaria, which possess no anus, are nevertheless much elongated forms.

To these facts of anatomy may be added a theoretical argument. In all animals which possess them, the specially digestive gland or glands, whose function is to secrete the juices which dissolve the nutritive portions of the food, are situated in connection with the first part of the alimentary canal. The greater part of the length of the canal—in those animals whose physiology has been best elucidated, and probably in others also—is destitute of any specially active secretion; its function is to absorb, and in the case of animals with branched alimentary canal to distribute, the foodstuffs which have been reduced to solution in the anterior part of the tract. The innutritious portions of the food are thus separated from the nutritive portions in the anterior part of the canal: if an anus exists, there is no reason why the undissolved innutritious portions should not pass along the tract, in company with the dissolved matters, to the anus, where they are expelled; but an anus is by no means necessary for this purpose, since, the mouth being nearer, there is little or no inconvenience in expelling the undigested residue by this exit. In other words, since there is no necessity for the undigested portions of the food to travel into the posterior part of the alimentary tract, it is unlikely that such a fundamental fact of structure as an anus should have been developed there for the purpose of allowing them an exit; and if an anus had not been independently developed for some other reason, solid food-remains would never have reached the posterior part of the intestine at all.

The original mode of expulsion of undigested food-remains in the Metazoa is by the mouth. To such a degree has this been impressed on the organism, that the faculty of such expulsion has never been lost. I imagine that it is within the personal knowledge of everyone that what may be called the remnant of this condition persists even in the highest forms—that the anterior part of the alimentary canal will still spontaneously return indigestible or undigested food through the mouth, instead of passing it on to be expelled through the hinder part of the tract. Reference may also be made to the faecal vomiting of intestinal obstruction, as showing how, on the occurrence of a check to the onward passage of solid matters even low down in the

intestine, the original condition of expulsion by the mouth is restored. The same thing is also seen in ruminants, where undigested food is returned to the mouth for purposes of mastication and reduction to a digestible form; and a similar condition is known pathologically in man under the name of mericism.

(2) If it is thus unnecessary to suppose that an anus was developed merely in connection with the expulsion of food-remains, it is also difficult to conjecture in what manner such an assumed development took place. The original condition would be that already indicated, in which the digestive juices act on the solid food in the anterior part of the tract, the soluble matters being extracted and passed on for absorption, the insoluble rejected by the mouth; and it is not easy to suppose that the undigested matters, originally retained, until expelled, in the anterior portion of the tract, gradually travelled further and further along the tract, and at last broke through at the posterior end, producing a mutilation which became hereditary in the race.

Indeed it is not easy,—in discussions, for example, of the origin of Annelids from Turbellarians,—to find any adequate description of the origin of the anus. MEYER, in his well-known paper on the origin of the Annelids (31), expressly begins with Turbellarians, that is, forms without an anus (“Die Vorfahren der Ringelwürmer stelle ich mir als kräftige, räuberische Turbellarien vor, welche pelagisch lebend seiner Zeit die Meere beherrschten”); but in the passage where one would expect to find described the origin of the anus, the ancestral forms have become “Turbellarian-like” animals which already possess one (“die turbellarienartigen Vorfahren der Anneliden . . . ähnlich den Nemertinen ein einfaches, hinten mit einem After endendes Darmrohr hatten”); the point is therefore altogether evaded. We have, in the anus, to do with what I have called “a fundamental fact of structure,” with an aperture which is comparable in anatomical importance to the mouth, is equally definite in position and relations, and arises by a similar process and frequently equally early in the ontogeny; and therefore it is not, I think, satisfactory to adduce, as the origin of the anus, the pores which in many Coelenterata and Turbellaria place the alimentary tract in communication with the exterior. Nor does LANG regard a similar suggestion of his own with any degree of confidence: he can only say that an anus must have been formed (27):—“Es ist zur Zeit noch unmöglich für den Enddarm und den After der Hirudineen bei den Plathelminthen Homologa anzufinden” (he is deriving Annelids by way of the Hirudinea from Platyhelminth forms resembling *Gunda segmentata*; the introduction of the Hirudinea in this connection has since been given up). “Vielleicht—es ist dies eine blosse Conjectur—hat sich einer der Excretionscanäle, die wir bei Polycladen vorfinden, specifisch entwickelt und zur Bildung des Enddarmes und der Afteröffnung Veranlassung gegeben. Jedenfalls darf das Vorhandensein eines Afters bei den Hirudineen uns nicht bestimmen, sie von den Plathelminthen weit zu entfernen. Einmal muss er sich doch gebildet haben! Auch die Nemertinen haben einen After, und doch fällt es Niemanden ein, sie aus dem Verbande der Plathelminthen loszulösen!”

In the latest presentation of his "Gunda-theory" (29), LANG does not refer to this point.

From what has been said it would seem to be neither necessary nor probable that an anus should have developed in order to permit the expulsion of undigested food-remains. In other words, the expulsive function of the posterior part of the alimentary canal is probably secondary; the anus was developed in some other connection, and its existence has merely been taken advantage of for getting rid of useless solid matters.

If the anus is not primarily an aperture for expulsion, can it be considered as primarily for ingestion? Is the inhalant function the original one?

(1) As a first point in favour of this suggestion may be mentioned the wide distribution of this inhalant function among those aquatic groups which possess an anus. The phenomena of ascending ciliary action and antiperistalsis give the posterior portion of the alimentary tract, as has been seen, a decidedly inhalant as distinguished from an expulsive character in the Polychæta and aquatic Oligochaeta; and a similar function of the intestine is recognised in the Archiannelida and Sipunculoidea, with some probability in the Echiuroidea, in the Echinoidea and Holothuroidea, the Mollusca (anal chamber of the Aplacophora), many Crustacea and Insecta, and even among the Chelonia. Intestinal respiration (in this case by means of swallowed air) is also known to occur in certain fishes.

(2) Again, as indicating the essentially inhalant character of the posterior aperture of the alimentary tract, may be mentioned the fact that tactile organs (sensory hairs) are in certain genera of aquatic Oligochaeta (*Slavina*, *Pristina*) almost or quite as numerous and quite as large round the anus as on the prostomium. In these forms also backward progression is as free and natural as forward progression. I have frequently been struck with this while examining these worms; the backward movement is not a recoil, or avoidance of something in front of the animal's head, but an active, purposeful, and continued locomotory effort, which is employed as often as or oftener than forward progression. In some specimens of *Dero* I have found a condition approaching that of certain Polychæta previously described (*cf.* pp. 806, 807). These may also be briefly again referred to in the present connection; it will be recalled that the intake of water by the anus, the eye-spots and evident tactile sensibility at the posterior end, the continual exploring movements, and the invariable progression with this end in advance, gave the morphologically posterior extremity the character of the physiological head of the animal.

(3) The facts of ontogeny may be adduced in this connection. If the anus originally subserved only the function of expulsion,—if it is to be considered as essentially centrifugally produced, as a breaking through, for the purpose of getting rid of matter,—it is difficult to see why its formation should be represented ontogenetically by an invagination from without. The idea may be perhaps better expressed as follows:—The anus exhibits in general a striking morphological similarity to the mouth in its mode of formation—it sometimes, indeed, arises in common with the mouth; and

it is not unreasonable to suppose that similarity or community of origin may indicate a primitive similarity or community of function.

(4) An argument against the view that the primary function of the anus was to act as a passage for undigested food, was that, holding this view, it is impossible to give any satisfactory account of its origin. Conversely, it will be an argument in favour of the opposite view—that the anus is primarily inhalant—if, on the basis of this view of its function, we can give a reasonable account of its first appearance.

Can we conceive that in an animal—for example, a Turbellarian—possessing a mouth and alimentary tract, in which the mouth serves for the intake of food both in mass and in solution, a new aperture was formed in a remote region of the body, for the purpose of introducing into another part of the alimentary tract a certain portion—let us suppose the fluid portion—of what previously entered at the mouth? The difficulties in the way of such a separate origin seem insuperable; indeed, it seems to be impossible adequately to explain the anus on any view, so long as it is considered to be a relatively recent formation, separate in origin from and arising at a later phylogenetic stage than the mouth.

We have, however, in SEDGWICK's theory (43) an explanation of the origin of the anus which satisfies our requirements. The theory views the anus as coeval in origin with the mouth, and as being an equally fundamental and essential fact of structure: it thus escapes the insuperable difficulties we encounter if we attempt to consider the anus as a later acquisition. While recognising the primarily inhalant character of the anus, it has moreover from my present point of view this advantage, that it was not evolved to meet the present case, but was independently enunciated in an altogether different connection,—in connection, namely, with the consideration of the origin of segmentation.

SEDGWICK, as is well known, derived both the mouth and anus of higher forms from a common aperture, which is represented in embryology by the blastopore, in comparative anatomy by the mouth-opening of the Actinozoa. Among the facts which SEDGWICK brought forward in support of the theory two may be briefly mentioned in the present connection: (*a*) that the mouth, or the anus, or both, are in the great majority of cases derived embryologically from the blastopore; (*b*) that even in the Actinozoa the mouth-aperture is, physiologically if not anatomically, divided into two by the approximation of the lips and locking of the cilia.

Briefly expressed, then, the theory supposes that the ancestor of the segmented Bilateria was of the Actinozoan type; that an elongation of the body took place in the direction of the long axis of the already oval or dumbbell-shaped mouth; that the mouth, now still more drawn out and slit-like, became divided into two apertures by the fusion of the lips across the middle, as occurs, for example, in the blastopore of *Peripatus* during development; and that in this way an elongated form resulted, with an oral aperture near one end and an anal aperture near the other, both apertures opening into a common gastrocoel. The original oral surface became the

ventral, on which progression took place, as happens sometimes in Actinozoa at the present day.

Obviously, since the undivided mouth aperture is primarily for ingestion (and for expulsion only secondarily, as a consequence of previous ingestion), the two resulting apertures will also primarily subserve the same purpose; that is, the anus will primarily be an inhalant aperture.

(5) A few collateral facts may, in conclusion, be adduced, which help to confirm the views here set forth.

(a) CARLGREN (11) has published some observations on the ingestion of food by certain Actinozoa. The cilia of the siphonoglyph or siphonoglyphs beat always in an inward direction, causing a corresponding current of water into the alimentary chamber. The entrance of solid food is occasioned both by cilia and by peristalsis of the stomodæal tube: in *Metridium* and *Sagartia* mainly by ciliary action; in *Caryophyllia* partly by peristalsis, which helps in the swallowing of large particles; while in *Tealia*, *Actinostola*, and *Bolocera*, peristalsis is the main factor. The undigested food-remains are particulate in *Metridium* and *Sagartia*, in which species they are got rid of by the action of cilia, which transport them from the stomodæum to the tips of the tentacles; in *Caryophyllia* the food-remains are brought up to the inner end of the stomodæum by the cilia of the filaments, and are then expelled by contractions of the body; in *Tealia* and *Actinostola* solid masses are expelled by contractions of the body, possibly assisted by peristaltic action of the stomodæum.

Thus in the Actinozoa the siphonoglyph is continuously engaged in introducing water containing matters, including oxygen, in solution; while solid food is introduced, and its remains expelled, through and by the agency of the muscular stomodæal tube. And we may perhaps follow out the line of thought indicated above by supposing that, of the two apertures into which the mouth-opening of the Actinozoa becomes divided, that which represents the end of and leads into the siphonoglyph becomes the anus: here there is always an inwardly directed ciliary current, which introduces water, but no solid food (compare the experiments on Polychæta in Part II., which show that the animals avoid ingesting solid particles by the anus, or speedily reject them if they are ingested). The other aperture, representing the main opening of the muscular stomodæum, becomes the mouth; here solid food is introduced, and here solid food-remains are expelled; in the primitive condition food-remains did not travel to the anus.

(b) The last point is one which has been referred to previously—the occurrence of digestive glands only in connection with the anterior part of the alimentary tract. This is an obvious consequence from the fact that solid matter is introduced only by the mouth: it is only this portion of the animal's food which requires to be acted on by digestive juices and so reduced to solution. It may be added, also, that jaws, teeth, and powerful muscular mechanisms are found only at the anterior end of the tract; and this for the same reason—it is only the nutriment which is introduced at the mouth that can require mechanical division.

It is commonly found, when any element of structure becomes split up in the course of evolution, that the resulting portions become differentiated anatomically, and take on different physiological functions. This has happened to the original mouth; but the specialisation of the two apertures which have resulted did not take place primarily in the way that at first sight appears most probable. The differentiation was not into an aperture for entrance and an aperture for exit; but into an aperture for the entrance of food in mass, and an aperture for the introduction of the fluid medium carrying oxygen and food-matters in solution.

A second line of thought is suggested by the statement on a previous page (p. 816), --that, so far as my observations go, it is only among the Nereidiformia (Rapacia) that families are to be found in which ascending ciliary action in the intestine certainly does not occur; in other words, this phenomenon is more universally prevalent among the sedentary and tubicolous than among the errant families.

I should be sorry to trust too far to this statement. My observations do not embrace all the families of Polychæta; it is very possible, therefore, that ascending ciliary action may be absent in some of the families of Sedentaria in which I have not been able to make any, or any satisfactory, observations; and, on the other hand, a more exhaustive investigation might have resulted in showing its occurrence among the Errantia in families in which I have not so far discovered it.

Proceeding, then, with this qualification in mind, I would observe that, according to the reasoning given above, ascending ciliary action is to be considered as a primitive character; and the question therefore arises, Are the Sedentaria—the division of the Polychæta in which this phenomenon occurs most markedly—the primitive Polychætes?

I believe that in all probability there exists no such thing as a primitive animal. Those that commonly go by this name are, if primitive in one or in some respects, much modified—either highly specialised or degenerate—in others. All that can be said is that certain animals are primitive in certain respects; but no animal of any group can be put down as primitive in all respects, just as no animal of a group can be said to be in all respects the “highest.” Still, some animals do undoubtedly show a larger number of primitive features than others; and in considering whether the sedentary Polychæta have not a better right to the title of primitive than the errant forms, all that we have to decide is whether or not, in the greater number of their more important features, they retain characters which we judge to be ancestral. No one, for example, would maintain that the tuft of feather-like gills which ornaments the anterior end of the sedentary Serpulimorpha was a primitive character, any more than a similar claim could be made for the perfectly shaped glass-like tube of the errant *Hyalinæcia*.

The view is perhaps generally current, that active free-living forms are more likely to be primitive, sedentary and especially fixed forms to be modified; and so far as I can gather, opinion seems rather against the view that the sedentary, especially the tubicolous, forms represent the primitive Polychæta. The usual representative of the

group in text-book and laboratory is *Nereis*, a typically errant form. The parapodia, the organs of active locomotion, are accepted as of the essence of Polychæte organisation: thus GOODRICH (22), deriving the Archiannelids from Chætopodous—presumably Polychæte—forms, speaks of the parapodia as having become “reduced”; so, too, FUCHS (19), defining the Cirratulidæ, speaks of the parapodia as being reduced (*reduziert*) to papillæ. And no doubt other indications of a similar view could be collected.

It is the other side of the argument that I here wish to present. First are the facts of the distribution of intestinal respiration, as evidenced by ascending ciliary action; these formed the starting-point for the present discussion, and need not be again alluded to.

Related to this phenomenon is the fact that in certain Sedentaria (pp. 806, 807) a very considerable physiological importance attaches to the posterior end of the body: the connection is illustrated further on p. 819. On SEDGWICK's theory, adopted in the present discussion, the physiological value of the two ends of the body would be at first—before any marked differentiation in favour of the head took place—approximately equal.

Next, we may briefly notice some points in connection with the vascular system. A dorsal vessel is present, as a rule, throughout the whole length of the body in errant forms. In sedentary forms it is usually present only in the anterior part of the body; posteriorly there exists a perienteric sinus, from which the dorsal vessel has not become differentiated; the blood in the sinus is propelled by antiperistaltic contractions of the muscular coat of the intestine.

These features are, according to the views put forward in the present paper, in great part primitive. The sinus is indeed perhaps a secondary character, and is to be looked on as derived from an irregular system of inter-communicating spaces by the disappearance of the partitions between them (*cf.* p. 778). But the non-differentiation of the dorsal vessel in the hinder portion of the body, and the propulsion of the blood in the sinus by antiperistaltic contractions of the intestine, are primitive features, which occur low down in the Oligochæte series (*Eolosoma*, Enchytræidæ, pp. 749, 752), and which represent early stages in the evolution of the vascular system.*

* It has been suggested to me that the condition in which the dorsal vessel exists only in the anterior region is probably correlated with the massing of the respiratory apparatus (the development of branchiæ) at the anterior end of the body. The examples of the *Eolosomatidæ* and *Enchytræidæ*, however, show that the differentiation, in the anterior region only, of a dorsal vessel may occur apart from such respiratory specialisations, and the same may be said of the *Opheliidæ* (*Polyophthalmus*) among the Polychæta.

That the two conditions—presence of a differentiated dorsal vessel only in the anterior region, and development of branchiæ at the head end—coexist in general in the Polychæta, is of course a fact, and it is highly probable that there is some relation between the two. But the correlation appears to me to be in a sense the reverse of that implied in the above suggestion. The necessity of providing a vascular supply for the gills restricts the gills, in general, to those parts of the body where the vascular system has reached a considerable degree of differentiation, with definite blood-vessels: in most of the Sedentaria this condition is only fulfilled at the anterior end of the body,—hence the development of gills in that region only. Forms in which definite vessels have been differentiated throughout the length of the body are not restricted to the anterior end as a site for their gills; so, for example, *Arenicola*, the *Spionidæ*, and other Polychæta, and so *Branchiodrilus* (*Chaetobranhus*) and *Dero* among the Naididæ, and *Branchiura* among the Tubificidæ.

With regard to the sedentary habit itself, it is possible to hold that this, rather than the active free-living condition, is primitive; and consequently that the absence of certain features, which when present are correlated with an active habit, may, in sedentary forms, be due not to degeneration, but to the persistence of an original state. The argument for the primitiveness of a sedentary habit has recently been presented by WILLEY (57): it would be superfluous, therefore, on my part to discuss the point, or even to repeat at length his presentation of the subject; all that can be done is to transcribe a few passages to indicate the character of his argument, and for the rest to refer the reader to his book.

WILLEY, writing from a physiological point of view, divides animals into phanerozoic (diurnal, positively heliotropic) and cryptozoic (crepuscular, nocturnal, and subterranean—in general terms, negatively heliotropic) forms, and states that the animal kingdom as a whole seems to show negative phototaxis. “A journey through any tropical forest or jungle, or even a little reflection, will, I think, suffice to convince one that while the vegetation is luxuriantly phanerotaetic, animal life is predominantly cryptotaetic. The jungle is like the desert and the ocean, to all superficial appearances frequently devoid of animal life. This is possibly not the impression which one would receive from the perusal of faunistic works; but it is certainly that which is produced by observations in the open, and I regard it as one of the radical bionomical or habitual differences between animals and plants.”

And later, “it is doubtless in virtue of this singular property of concealment that so many of the primitive forms (he is speaking of the Arthropoda) have survived at the present day to be at once the delight and bewilderment of the systematist.” “Predatory aquatic animals . . . may be described as phanerozoic; but we may confidently assert that in all cases a definite cryptotaetic bias of varying intensity could be demonstrated.” Finally, “the basic quality underlying all animal life is the cryptic, the fear of the sun.”

This tendency to concealment is, of course, related to the sedentary habit; but about the latter there is more to be said. “The remarkable prevalence of the sedentary habit amongst the lower (*i.e.* invertebrate) animals seems to indicate that something peculiarly primordial lies at the back of the phenomenon.” Fixation is an extreme form of the sedentary habit; the principle which lies at the back of both is expressed in the term “stereotropism” (*i.e.* the tendency to cling to a surface), invented by J. LOEB.

“Many cases amongst the Annelid worms could be instanced where stereotropism and pleotropism (the free-swimming habit) exist side by side, the latter frequently only manifesting itself at the breeding or swarming season, as with epigamous Nereids.” EISEN’s observations have shown that free swimming results from a greater violence of the same movements that are used in crawling; “when the amplitude of these undulations surpasses a certain magnitude, the rapidity of movement is thereby increased to such an extent that the animal rises from the bottom and swims through the water.” Eisen concludes that the stereotropic movement (on the bottom) is secondary as compared with the pleotropic movement (through the water), and is derived by

inheritance from swimmers; in the same strain, referring to *Amphioxus*, he says that however primitive one may hold its organisation to be, yet nobody will assert that its limbless body and its predominantly cryptozoic locomotion represent archaic features.

WILLEY, however, disagrees with EISIG: "I am unable," he says, "to follow these conclusions myself, as I approach this matter independently from a cryptozoic and stereotropic standpoint"; WILLEY would thus presumably derive the free-swimming habit of, say, *Phyllodoce*ids from crawling locomotion, of which it would merely be an exaggerated development. Finally, he reaches "the conclusion that just as all divisions of the animal kingdom display a cryptozoic bias, so do they all show a statozoic tendency" (Statozoa = sedentary animals). "The sedentary habit is referable to a stereotropic basis, and pelagic or pleotropic forms belonging to groups which are predominantly sedentary, have had a probable statozoic origin."

If the above line of reasoning is correct, the absence of parapodia, *i.e.* of organs of active locomotion, in the sedentary forms will not be, as is perhaps generally assumed, due to degeneration; it will be a primitive feature. In other words, the sedentary Polychæta have never had parapodia. And, in fact, well-developed parapodia occur in only a relatively small minority of the families of Polychæta; and in these again it is only a portion which have the double-branched parapodium, consisting of notopodium and neuropodium, which, in the form in which it occurs in *Nereis*, constitutes the type of the organ which is presented to the student. Parapodia (I refer, of course, to the outgrowths of the body-wall, not to the setæ) are, moreover, quite unrepresented in the related groups of the Archiannelida and Oligochæta. From the facts of their occurrence, therefore, it would appear that they represent a development within the Polychæte stem, and have attained to their full size and differentiation in only a few of the topmost branches of that stem.

But if the parapodia are a secondary and a comparatively late development, it need hardly be said that the same is not the case with the groups of setæ which accompany them. These are found, in corresponding positions, in certain of the Archiannelida and in all Oligochæta, and represent, therefore, a character of the common ancestor of the Chætopoda. They are the primary locomotor organs; in general, the animal works itself along by securing a hold on the substratum by means of its setæ, and then using them as levers. The degree of activity possible to the animal is determined by the size and strength of the setæ and the degree of development of the muscles which work them, and is thus correlated with the presence and size of the parapodia. The typical positions for the groups of setæ are dorsolateral and ventrolateral; it can hardly be doubted that in many earthworms, where the dorsal bundle is placed at the level of or below the horizontal diameter of the body, we have to do with a secondary shifting.

It follows from the manner in which the setæ are employed, that in the material environment of the ancestral Chætopod there must have been something for the dorsolateral setæ to work upon, equally with the ventrolateral; and this could only be

the case with animals living in crevices, with the dorsal surface covered over in some way; there would otherwise have been no possibility of the dorsolateral setæ obtaining the purchase which is necessary for their effective use. It appears necessary to suppose, therefore, that the ancestors of the Chaetopoda, and the original representatives of both of the larger groups (Oligochaeta and Polychæta), lived in crevices or crawled about under cover—were, to use WILLEY's term, cryptozoic.

In the course of evolution the sedentary habit which is associated with the cryptozoic life became in some representatives of the Polychæta more pronounced: these developed into such tubicolous forms as the Serpulids, whose large feather-like gill-tufts are an adaptation to an extreme form of sedentary existence. In other members of the group the sedentary habit was to a considerable extent, or at certain periods of the life-history, altogether abandoned. In correlation with the assumption of more active habits, the muscular mechanisms of locomotion became better developed; and the result has been the appearance of distinct parapodia,—projections, largely muscular, of the body-wall,—associated with the setæ, the primary locomotor organs: an interesting parallel is seen in certain Rotifers with highly developed locomotor capabilities, where seta-like hairs are accompanied by muscular excrescences of the body-wall resembling parapodia. In extreme cases the lobe-like parapodia themselves are more effective as locomotor organs than the setæ, since they can be used as oars in swimming movements through the water; one may recall EISIG's observations, quoted by WILLEY (*vide ante*), that swimming locomotion through the water results from a greater violence of the same movements as are executed in crawling. In *Tomopteris* the setæ have disappeared along with crawling locomotion, and the animals are pelagic.

To turn for a moment to the Oligochaeta: the earthworms are noteworthy because, as has been mentioned, the dorsolateral group of setæ has sunk down to, or below, the horizontal diameter of the body. What the occasion of this was, it is difficult to conjecture; it does not seem very probable that on taking to a terrestrial existence the evolving earthworms abandoned the cryptozoic mode of life so far as to adopt the habit of creeping mainly on the surface, and not in crevices. But whatever the occasion may have been, it is interesting to observe that the latest modification of setal distribution restores the original condition, in which a number of setæ were situated in the dorsal quadrants of the body-circumference,—though with a difference. In many, indeed in the majority, of the Megascolecidae, the most highly differentiated and most variable family of earthworms, the setæ have broken loose from their customary positions, and have spread in a more or less complete ring all round each segment,—a perfect adaptation to the cryptozoic habit, to life in crevices.

It will be admitted that probably no single representative of the present-day Polychæta comes anywhere near the ancestral form, and that both errant and sedentary branches have diverged, perhaps widely, from their common progenitor. In each branch certain primitive features have been retained; in each branch certain secondary

modifications have arisen. Thus the Sedentaria are modified, as compared with most errant forms, in the frequent reduction in number of the nephridia, in the differentiation of the body-segments so as to form two or even three distinct regions, and in the great development of the respiratory apparatus at the anterior end. But the purpose of the last few pages will have been accomplished if, by the considerations I have adduced, I have been able to show that the more sedentary Polychæta retain a number of ancestral characters :—(1) in their sedentary and markedly cryptozoic habit ; (2) in the correlated absence or slight development of the parapodia, and in the absence of jaws and teeth ; (3) in the anatomy of the circulatory system ; (4) in the general occurrence of intestinal respiration, and perhaps in the greater physiological value of the posterior end of the body,—and, though these characters will make their appeal with different degrees of force in different cases, to render it probable that the Sedentaria have a better right than the errant members of the group to be recognised as the present-day representatives of the ancestral form.

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